GENETICS OF PLANT ARCHITECTURE AND ITS EFFECT ON YIELD IN CASSAVA (*Manihot esculenta* Crantz)

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THIS THESIS IS SUBMITTED TO THE UNIVERSITY OF GHANA, LEGON IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE AWARD OF DOCTOR OF PHILOSOPHY DEGREE IN PLANT BREEDING

WEST AFRICA CENTRE FOR CROP IMPROVEMENT

COLLEGE OF BASIC AND APPLIED SCIENCES

UNIVERSITY OF GHANA

LEGON

JUNE, 2024

DECLARATION

I hereby declare that except for references to works of other researchers, which have been duly cited, this work is my original research and that neither part nor whole has been presented elsewhere for the award of a degree.

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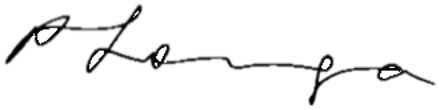

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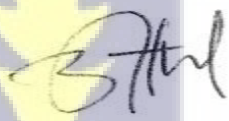

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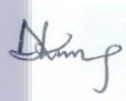

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ABSTRACT

Cassava (*Manihot esculenta* Crantz) is a significant starch source for various industrial applications. However, cassava's traditional cultivation and harvesting methods are labour-intensive and inefficient, limiting the supply of fresh cassava roots for industrial starch production. Cassava cultivars with compact plant architecture and moderate plant height are required to increase the productivity and quality of fresh cassava roots through mechanical farming. Plant architecture-related parameters such as plant height, height at first branch, harvest index, branching level, stem diameter, branching angle, and lodging tolerance are crucial for crop yield and adaptability to mechanized cultivation. However, the genetics of cassava plant architecture still need to be better understood. The purpose of this study was to determine the genetic bases of the plant architecture, yield and productivity-related traits in cassava, especially starch content. A panel of 434 cassava clones developed at the International Institute of Tropical Agriculture, Nigeria, was genotyped and phenotyped for 17 plant architecture, yield and productivity-related traits at four locations across four growing seasons in Nigeria. which constitute five test environments. A genome-wide association study (GWAS) was conducted using the phenotypic data from a panel of 434 clones and 54,574 high-quality DArTseq-derived SNP markers evenly distributed across the cassava genome. Significant associations between 17 SNPs and eight plant architecture and yield component traits were identified through GWAS. Out of these 17 SNPs, 13 were linked to 18 putative candidate genes for seven traits including angle of branching (4), plant type (4), overall plant appearance (2), level of branching (4), harvest index (3), and number of harvested plants (1). These candidate genes exhibit various functions in relation to plant architecture, adaptation, yield, plant growth, development, stress response, and starch metabolism. One of the 18 putative candidate genes identified in this study is a novel gene (Manes.01G077900). This represents a significant contribution to knowledge. The effect of genotype by environment interaction on the stability of genotypes was evaluated using the AMMI (Additive Main Effects and Multiplicative Interaction), Finlay-Wilkinson, and GGE (Genotype Main Effects and Genotype by Environment Interaction) biplots while the test environments were delineated into mega environments using statistical models such as AMMI (Additive Main Effects and Multiplicative Interaction), and GGE (Genotype Main Effects and Genotype by Environment Interaction) biplots. The genotypic main effect showed sufficient variation that could be exploited for genetic gains, but the interaction between genotype and environment could complicate this.

Two cassava accessions with erect plant type G424 (TMS18F1436P0049) and G83 (TMS18F1096P0013) were found to be adaptable and stable for fresh root yield and starch content, making them early selection candidates for these traits. The prospect of adopting the use of near infrared spectroscopy data obtained using the affordable SCiO sensor spectrometer in predicting starch and dry matter content from fresh cassava roots was evaluated. The results obtained from this research produced identical results to the prediction metrics that were reported in previous trials with respect to the consistency and accuracy of spectra (NIRS) data that were obtained using SCiO sensor spectrometer. The results validate the previous findings with desirable accuracy of prediction. A high throughput phenotyping procedure that enhances the rapid and cost-effective estimation of plant architecture and yield traits in cassava was developed using normalized difference vegetation index (NDVI) data obtained using an affordable handheld sensor manufactured by Trimble. Two models (linear regression and polynomial regression model) were used in developing phenotyping protocols for predicting yield and plant architecture traits in cassava using NDVI data. The polynomial regression model showed similar prediction accuracy for fresh root yield across two environments at 3, 6, and 9 months after planting. The linear regression model used NDVI data to predict yield or plant architecture traits directly. Based on prediction accuracy, there exist a significant disparity between NDVI data obtained from the two trial locations (Mokwa and Onne), this affirms the effect of the significant genotype by environment interaction on the performance of the cassava accessions across the test environments. The cassava accessions that combine the desirable plant architecture traits, high yield and more than 25% starch content would be selected for further evaluation at the advanced yield trial (AYT) stage and subsequent stages of the cassava improvement program.

DEDICATION

If it had not been the Lord who was on my side, this thesis would not have been possible. I return all the glory and honour to Him, for He is good and His mercy endures forever. All praise be to God.

ACKNOWLEDGEMENTS

I am deeply grateful to the Lord for His goodness, mercy, and grace, which enabled me to complete this journey successfully.

I extend my heartfelt appreciation to my in-country supervisor, Prof. Chiedozie Egesi, for granting me the opportunity to conduct my research under his guidance on the NextGen Cassava Breeding Project. His magnanimity and mentorship have been invaluable. My thanks also go to my amiable mentors, Dr. Ismail Rabbi and Dr. Gaby Mbanjo, who worked closely with Prof. Egesi in supervising my research. I am profoundly grateful to my supervisory committee, Prof. Pangirayi Toongona, Prof. Samuel Kwame Offei and Dr. Daniel Dzidzienyo for the excellent training, guidance and mentoring, which were crucial in refining my research thesis and enhancing my writing skills. Special thanks to Prof. Eric Yirenkyi Danquah, the Director of the West Africa Centre for Crop Improvement (WACCI), for his leadership, guidance and immense support to my family and I.

I express my immense gratitude to the German Academic Exchange Service (DAAD) for granting me a full scholarship for my PhD program and sponsoring my short course and capacity-building program in Germany. My thanks also go to the NextGen Project, sponsored by the Bill & Melinda Gates Foundation and the UK Department for International Development (DFID), for providing access to state-of-the-art facilities for my research.

I sincerely appreciate the support and love from all the staff of the cassava breeding unit at the International Institute of Tropical Agriculture (IITA) Ibadan, Ikenne, Onne, Mokwa, and Kano Stations.

I am deeply thankful to my loving, caring wife and senior colleague, Dr. Olayinka Adesike Oladoyin and my wonderful sons, Olayinka Adedamola Oluwajare, Olayinka Adedayo Oluwajoba and Olayinka Adedapo Oluwajuwonlo for their support, understanding, patience, and sacrifice during the past four and a half years. I am truly grateful. Finally, my profound appreciation goes to my parents for their love, care, and support from my cradle to this moment. I appreciate all their investment in my life. To my siblings, thank you for all the sacrifices and love you have extended to me.

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LIST OF ABBREVIATIONS

ACMV *African Cassava Mosaic Virus*

BIC Bayesian Information Criterion

BLUP Best Linear Unbiased Prediction

CBBD Cassava Bacteria Blight Disease

CIAT International Center for Tropical Agriculture

CMD Cassava Mosaic Disease

DArT Diversity Array Technology

FAO Food and Agriculture Organization

FAOSTAT Food and Agriculture Organization of the United Nations' Statistics Division

FOREX Foreign Exchange

GWAS Genome-Wide Association Study

IITA International Institute of Tropical Agriculture

IRECI Infrared Emission Chlorophyll Index

NDVI Normalized Difference Vegetation Index

NEXTGEN Next Generation Cassava Breeding Project

NIRS Near-Infrared Reflectance Spectroscopy

PYT Preliminary Yield Trial

QTL Quantitative Trait Loci

RVI Ratio Vegetation Index

SAVI Soil Adjusted Vegetation Index

CHAPTER ONE

1.0 GENERAL INTRODUCTION

Cassava (*Manihot esculenta* Crantz) is a heterozygous, clonally propagated crop suitably adapted to tropical and subtropical regions. An average of 500 million people in Africa rely on cassava to meet their daily calorie needs. After maize, cassava is Africa's second most important crop (Amelework & Bairu, 2022). According to Fregene (2021), cassava's growing popularity and acceptability in Africa could be attributted to some of the inate attributes of the crop viz: it can be kept on farms for strategic planning during emergency situations, it can also serve as a backup for rescue during food shortages, or during the off-season. Cassava production is estimated at 303 million tons, and more than half of this is produced in Africa (FAOSTAT, 2021). About 19% of the world's fresh cassava root production comes from Nigeria, the country that produces the most cassava (FAOSTAT, 2021). Cassava is a multipurpose crop. "Cassava is the foundation of food security and agricultural development in Nigeria, and the country's health is inextricably tied to the health of its cassava" (Egesi, 2020). It is an essential crop in a low-income economy like Nigeria. It constitutes a cheap source of nutrients and calories. The fresh starchy root can be eaten raw or boiled, processed into a sticky dough (Fufu), or fermented and roasted into flour (Gari). It can also be processed into African salad (Abacha), noodles, bread and beverage (Tapioca). Cassava chips constitute a vital component of livestock feeds. A wide range of essential industrial products are derived from cassava: adhesives, liquid glucose, biodegradable plastics, bioethanol, starch, and syrup (Parmar *et al*., 2017; FAOSTAT, 2021).

Cassava starch, derived from fresh cassava roots, is a crucial raw material for various industries, including food, beverage, pharmaceuticals, paper, and textiles. Its superior quality and cost-effective production process make it a popular choice for healthier diets (Holdings, 2018; FBI, 2020). The global market size of cassava starch is expected to reach $66.84 billion by 2026, with Nigeria's share of (0.29%) at $118.81 million in 2021 despite being the leading producer of fresh cassava roots globally (DBMR, 2020; FBI, 2020). The country imports about 1.7 million metric tons of starch, costing about $26.7 million and $23.3 million worth of sweeteners annually (Adewunmi, 2019). Nigeria faces challenges in maximizing cassava starch production due to high

cost of producing fresh cassava roots, inadequate processing facilities, and infrastructure (Adewunmi, 2019; Sanni, 2019). Achieving sustainable production of cassava starch in Nigeria can be a low-hanging fruit for the government to boost its economy through improved forex earning. Cassava is also crucial for reducing food importation bills in African countries, particularly Nigeria (Fregene, 2021). By investing in cassava cultivation and processing, African nations could save $35 billion in food import costs. Cassava is adaptable, resilient against climate change, and provides nutritional security and employment opportunities. Prioritizing cassava consumption, processing, and farming is essential for reducing food import costs (Fregene, 2021). The demand for fresh cassava roots in Nigeria is increasing gradually and is forecast to quadruple due to population expansion, which is estimated to double by 2050 (United Nations, 2019).

Although Nigeria's production of fresh cassava roots has increased steadily over the last 24 years, this increase was made possible by an annual increase in the amount of land used for cassava cultivation rather than an increase in productivity per unit area (FAOSTAT, 2021). To achieve a sustainable increase in the production of fresh cassava roots in Nigeria, improved technology should be introduced to increase productivity on farmers' fields. The current average yield of 8 tons per hectare (t/ha) of fresh cassava yield in Nigeria could be increased to 22 tons per hectare (t/ha) obtained by farmers in Thailand and Ghana (FAOSTAT, 2021). An example of such technological injection is the mechanized method of producing fresh cassava roots, which has worked effectively in Thailand. This technology was complemented by biological technology in the form of the availability of several improved cassava varieties that are suitable for mechanized cassava cultivation (Kawano, 2003; Thepent, 2015; Soni, 2017; Cramb & Thepent, 2020). It is anticipated that adopting these innovations will enhance the output of fresh cassava roots in Nigeria (Ceballos *et al.*, 2010; Shetty *et al.*, 2014; Mabayoje, 2017). The NextGen Cassava Program developed two new cassava varieties in 2020: Game Changer and Obasanjo 2. These cultivars were released especially to replace the industry-standard cassava variety TME 419. These varieties were developed in response to a growing awareness of the need to have cassava varieties that are appropriate for mechanized farming. This is critical in optimizing the production of fresh cassava roots for industrial use.

Despite recent accomplishments, existing cassava varieties have not yielded the desired transformative impact on stakeholders involved in the cassava starch value chain. It is essential to develop additional varieties that can enhance productivity and maximize profits for end users.

While reviewing the breeding activities of the International Center for Tropical Agriculture (CIAT) in over fifty years, Ceballos *et al*. (2021) noted that breeding goals have shifted from yield and starch content to include traits that determine the growth habit (plant architecture) of cassava plants. These plant architecture traits are receiving more attention, and much emphasis is being placed on traits that enhance suitability for mechanized cultivation, such as compactness and erectness. This is in line with the advances made in Asia, where cassava breeders have developed high yielding cassava cultivars ideal for mechanized farming (Malik *et al*., 2020).

Plant architecture is an important determinant of the overall performance of crop plants (Fourcaud *et al*., 2008; Mathan *et al*., 2016). Apart from its crucial role in determining crop productivity, it is vital in determining the ease of crop cultivation, management and adaptability to mechanized farming (Mathan *et al*., 2016). Being a vegetatively propagated crop, the stem length, ease of storage and shelf life of cassava stems are essential plant architecture traits desired by the farmers; they prefer erect plants that guarantee these features (Ceballos *et al*., 2016, 2020). The genetic basis and inheritance patterns of plant architecture in cassava are poorly understood (Ceballos *et al*., 2004). Having a comprehensive understanding of the genetics of plant architecture in cassava as it relates to increased yield (Srisawad *et al*., 2023), improved quality traits such as starch content (Amelework & Bairu, 2022), and suitability for mechanized cultivation (de Oliveira *et al*., 2020), would enhance and fast-track the development of improved cassava varieties with ideal plant architecture optimized for domestic and industrial use (Ceballos *et al*., 2020). The potential yield of cassava is influenced by several plant growth and architectural factors, including root development, and canopy architecture (Murchie & Burgess, 2022), photosynthesis and radiation use efficiency (De Souza *et al*., 2017), leaf area and disposition (Moreno-Cadena *et al*., 2021). The architecture of a plant is shaped by its genetic makeup, which affects starch content and crop productivity (Cai *et al*., 2016). A few characteristics that influence the overall plant architecture of cassava include the plant's height, branching pattern, height at which the first branch appears, level of branching, stem thickness, angle of branching, overall plant type, canopy cover, and leaf size. These traits greatly influence how well cassava grows, adapts to different environments, and its overall performance (Veltkamp, 1985; Santanoo *et al*., 2020). Significant correlation between plant architecture and productivity related traits have been reported in several crop species (Lauri & Lespinasse, 2001; Rymaszewski *et al*., 2017). Previous studies have suggested that optimizing of plant architecture could significantly increase the yield of crops

(Huang *et al*., 2016; Mathan *et al*., 2016). More recently, Adu *et al*. (2018) reported significant variation among cassava genotypes and highlighted the effect of plant architecture features on cassava productivity. Cassava breeders in Brazil have developed a few cassava varieties with ideal plant architecture, making them suitable for mechanized cultivation and increased productivity (Carvalho *et al*., 2011; Vieira *et al*., 2018, 2020). However, to manipulate the plant architecture traits for enhanced productivity and mechanized cultivation, it is important to understand the genetic basis of these traits (Reinhardt & Kuhlemeier, 2002; Barthélémy & Caraglio, 2007).

It is imperative to adopt a comprehensive approach in the development of cassava varieties with improved starch and dry matter content and compatibility for mechanized cultivation to increase the productivity of fresh cassava roots for industrial use in Nigeria. Much thought should be given to plant architecture as the focal point of the overall improvement we seek (productivity, mechanized farming, and source of commercial planting material).

Fortunately, cassava can be farmed all year long in the nation's many agro-ecological zones. As a result, it will be necessary to assess the effects of environmental factors on plant productivity, as well as the genetic factors that underpin the quantified genetic variations. Unfortunately, relatively limited research has been conducted by cassava breeders to understand the genetics of plant architecture and its effects on yield and quality traits like starch content (Okogbenin & Fregene, 2003; Moreno *et al*., 2016; Srisawad *et al*., 2023). Using full sib biparental mapping populations of 92, 133 and144 individuals respectively, Srisawad *et al*. (2023), Moreno *et al*. (2016) and Okogbenin & Fregene (2003) detected some quantitative trait loci (QTLs) for architecture traits. These authors suggested further expansive studies should be conducted to unravel robust genetic underpinnings of the plant architecture and yield traits in cassava. The use of biparental mapping population in QTL discovery is associated with the following shortcomings: a) lower resolution, b) restricted genetic base, c) need to develop a specific mapping population; it is time consuming and expensive d) only two alleles could be assessed per time (Collard *et al*., 2005; Semagn *et al*., 2006; Mitchell-olds, 2010). However, more stable QTLs for essential cassava traits have been discovered using genome-wide association studies (GWAS) on a population of cassava accessions (Esuma *et al*., 2016; Wolfe *et al*., 2016; Kayondo *et al*., 2018; Ikeogu *et al*., 2019; Rabbi *et al*., 2020).

The application of molecular techniques in crop improvement has enhanced the speed of breeding through fast and reliable sequencing of the genetic make-up of crop plants. However, due

to a lack of complementarity in terms of improved capacity and speed of phenotyping protocols in handling thousands of breeding entries at once, the advantages provided by these techniques have been underutilized. A couple of high throughput phenotyping procedures, such as near-infrared reflectance spectroscopy (NIRS) and normalized difference vegetation index (NDVI), have been deployed in the rapid evaluation and accurate prediction of quality and yield traits in crop plants. NIRS technology has been evaluated for several purposes, including quantification of nutrient contents in food crops (grains, roots and tubers), (Montes *et al*., 2013; García-sánchez, 2015; Johnson & Walsh, 2020), assessing dry matter content and cyanogenic potential (Sánchez *et al*., 2014), starch content (Maraphum, 2020), beta carotene and total carotenoid content in cassava (Ikeogu *et al*., 2019) as well as estimating texture and cooking time of common beans (Wafula *et al*., 2020). This technology has been used in the *in-vivo* estimation of chlorophyll contents in leaves (Li *et al*., 2019) and selecting rice seed mutants from a seed lot exposed to mutagenic treatments (Jankowicz-Cieslak *et al*., 2016). The use of NDVI data extracted from multispectral sensors mounted on unmanned aerial vehicles has been instrumental in accurate yield prediction, with the silking stage in maize, Sanodiya *et al*. (2017), early reproductive and late ripening stages in rice and middle reproductive to early ripening stages in wheat Guan *et al*. (2019) being identified as the most reliable phenological stages for prediction.

Main objective:

The main objective of the study was to improve cassava productivity through genetic manipulation of plant architecture.

Specific objectives:

The specific objectives of the study were to:

1. Identify loci and candidate genes associated with starch content, plant architecture, and yield traits.
2. Assess the effect of the environment on plant architecture and yield traits.
3. Validate a high-throughput phenotyping protocol for estimating starch and dry matter content using near-infrared spectroscopy (NIRs).

4. Develop accurate and high-throughput phenotyping protocols for evaluating yield and plant architecture traits in cassava.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Origin of cassava and distribution

Cassava (*Manihot esculenta* Crantz) belongs to the Euphorbiaceae family. It has a complex evolutionary and agricultural history that involves both its botanical origin and its domestication. Botanical origin refers to the geographical regions where the wild ancestors of cassava naturally evolved and diversified. Domestication refers to the process and location where early human settlements began cultivating cassava, selecting for desirable traits and transforming it to suit their use. Regarding the crop's origin, three different theories have drawn a lot of interest. These are of botanical, geographical, and agricultural origin. While geographical origin focuses more on the region of diversification, agricultural origin addresses concerns about the areas where the wild progenitors were first cultivated, the focus of botanical origin is the existence of the wild relatives (Allem, 2009). The distribution pattern and regional prevalence of morphologically identical relatives of the crop indicate that cassava originated in four distinct areas: "Guatemala and Mexico; the coastal savannahs of northwestern South America; eastern Bolivia and northwestern Argentina; and eastern Brazil" (Spath, 1973). The crop is thought to have originated primarily in Brazil and Paraguay (O'Hair, 1995).

In contrast to its broader botanical origin, the domestication of cassava is thought to have occurred in a more specific region. Allem (1994) identified Goiás, in central Brazil, as a likely center of domestication, based on the presence of both wild and early cultivated forms. Later, Allem (2009), refined this view, suggesting that the southwestern Amazon Basin, encompassing parts of Brazil, Bolivia, and Peru was the primary center where cassava was first domesticated. This region provided the ecological and cultural conditions necessary for early human communities to begin cultivating and selecting cassava for traits such as reduced toxicity and increased starch content.

Joaquim *et al*. (2001) conducted phylogenetic analysis on cultivated cassava accessions, wild relatives, and related taxa using SSR markers. They found a strong link between *Manihot esculenta ssp. flabellifolia* and *Manihot esculenta ssp. peruviana*, confirming their association with the same taxon. This aligns with the findings of Olsen & Schaal (1999), who opined that *Manihot*

esculenta ssp. flabellifolia was the sole progenitor from which cassava was domesticated. Olsen & Schaal (2001) proposed that the southern border of the Amazon basin is the singular center of origin of cassava. The outcome of this research also affirmed their previous position that *Manihot esculenta ssp. flabellifolia* was the sole progenitor from which cassava was domesticated. However, this contradicts Lebot's (2009) assertion that cassava is an interspecific hybrid. In terms of which one comes first, Lebot (2009) posited that sweet cassava cultivars predate bitter cultivars, with sweet varieties mainly cultivated in the eastern region of South America and bitter varieties dominating West and Central America and Mexico. However, the introduction of cassava to Africa occurred in the sixteenth century through the incursion of the Portuguese Nweke (2005), but its popularity soared in Nigeria due to technology transfer and the return of enslaved individuals to their homelands (Adeniji *et al*., 2005). By the seventeenth century, the popularity and acceptability of cassava in Africa had grown significantly (Jones, 1969). Cassava has now been introduced to all countries along the world's tropical belt, where it has become an essential component of the economy and food systems (Lebot, 2009).

2.2 Production Overview, Yield Gaps and Comparative Analysis of Nigeria's Cassava Industry

Cassava has a global production figure of about 303 million tons, making it the sixth most produced food crop in the world, after rice, maize, wheat, soybean, potato, and sugarcane (FAOSTAT, 2021). More than half of this output is accounted for in Africa, where the crop is critical to the survival and well-being of over 300 million people (IITA, 2021). Nigeria, the crop's leading producer, accounts for approximately nineteen percent of global production (FAOSTAT, 2021). Significant rise has been observed in the production of fresh cassava roots in Africa (Ceballos *et al*., 2017). Population pressure and low-income households' urgent need for a cheaper source of calories in the face of rising poverty are the key factors that engendered the boost experienced in the production of fresh cassava roots. The crop's versatility and multipurpose use for fresh and processed products for human consumption, animal feed and industrial raw material are responsible for the recent overwhelming increased demand for fresh cassava root and the urgent need to address the yield gap to increase fresh cassava root productivity per unit resource. To address the issue of the yield gap, the methods of producing fresh cassava roots must be carefully considered. Farmers in Africa produce more than fifty percent of fresh cassava roots; smallholder farmers with average farmland of one hectare and a heavy reliance on primitive tools and a cultural

crop production system produce approximately 95 percent of fresh cassava roots produced in Nigeria (Sabo *et al*., 2018).

Nigeria and Thailand are leading producers of fresh cassava roots globally, but the yield per hectare on farmers' fields in Thailand is nearly twice that obtained on farmers' fields in Nigeria (13tons ha^{-1}) (FAOSTAT, 2021). The sharp disparity observed in the level of productivity attainable on farmers' fields between these two countries could be linked to the end-use of the fresh cassava roots (Ceballos *et al*., 2012). Cassava is widely consumed as a staple in Nigeria, whereas it is a major industrial crop with significant export and foreign trade potential in Thailand (FAOSTAT, 2021). In Thailand, as an industrial crop, there is an organized market with consistent demand and a guaranteed profitable return on investment for farmers. This factor has resulted in a consistent annual increase of about 0.5 tons ha^{-1} in cassava yield per unit area in Thailand, compared to a 0.09 tons ha^{-1} annual increase in yield in Nigeria between 1990 and 2012 (FAOSTAT, 2021). Another important factor contributing to the yield disparity between farmers in Nigeria and Thailand is the aspect of optimizing overall productivity and long-term production stability, which could be accomplished through improved yield, improved plant architecture, improved quality traits, long-term resistance to major diseases, and tolerance to key pests (Ceballos *et al*., 2010).

Despite being the leading producer of fresh cassava roots in the world, the low yield of fresh cassava roots per hectare on farmers' fields in Nigeria keeps escalating the gap in yield compared to countries like Thailand and Brazil. Nigeria's cassava yield gap challenge is more of systemic failure rather than agronomic. Three major causes of yield gaps were highlighted in this section: (1) inadequate integration of research innovations into smallholder farming systems, (2) absence of a strong market-driven production structure comparable to Thailand's industrial cassava sector and (3) limited progress in breeding and deploying varieties optimized for both yield and industrial use. Addressing these gaps is critical to enhancing cassava's contribution to food security, industrial growth, and sustainable rural livelihoods in Nigeria.

2.3 Cassava production constraints

Waddington *et al*. (2010) classified the sources of constraints to major crop production into four primary groups: managerial, biotic, abiotic, and socioeconomic factors. The authors proposed that these factors were to blame for the large yield gaps reported from farmers' fields.

Several biotic and abiotic factors have been identified as contributing to Nigeria's subpar cassava on-farm yield (IITA, 1990, 2021). One major biotic constraint to cassava production is the cassava mosaic disease (CMD). Its level of severity is determined by the crop variety, phenological stage of infection, and pathogen virulence. Sub-Saharan Africa has recorded yield losses ranging from a few to no tubers produced (Alabi *et al*., 2011). Crop loss may occur from severe cases of cassava mosaic disease (CMD) (Bisimwa *et al*., 2015) and cassava bacteria blight disease (CBBD) (Waisundara, 2018).

Other biotic factors include: cassava mealy bug (*Phenacoccus manihoti*) which can cause a 60% loss of fresh cassava roots (Neuenschwander, 2005), while cassava green mite (*Mononychellus tanajoa*) can cause a 40% yield loss (Pollangyo & Odour, 2013). Yield losses due to nematode infestation (*Meloidogyne incognita and M. japonica*) could be as high as 50% (Akinsanya *et al*., 2020). Uncontrolled weed infestation may result in a 25% loss in fresh root yield and total crop loss in some instances (Hauser & Ekeleme, 2017). Ceballos *et al*. (2010) outlined the severity of the economic damage caused by the major biotic constraints on cassava production. The authors described extensive breeding interventions and progress made in reducing pest and disease outbreaks. Researchers agreed that climate change do not pose a direct threat to cassava adaptability and productivity, but concerns were raised that it could disrupt the cassava pest and disease complex, necessitating the need to develop and deploy more resilient and climate-smart cassava varieties for farmers' use (Ceballos *et al*., 2010). Significant progress has been made on this; one notable example is the identification of cassava varieties that contain the cassava mosaic disease resistance gene (Houngue *et al*., 2019). Ezenwaka *et al*. (2020) have discovered an unusual QTL region on chromosome 12 that contains nine genes that have the potential to confer resistance to cassava green mite infestation, enhance leaf pubescence and stay green.

In addition to biotic constraints, ease of access to labor and affordability have been identified as essential factors influencing farmers' yield differentials (Fermont *et al*., 2009). Fermont *et al*. (2009) identified weed control as a critical and capital-intensive farm management activity. According to them, if not given due attention, the weed challenge could cause yield losses of up to 11.6 tons ha^{-1} on farmers' fields. In the same vein, Waddington *et al*. (2010) outlined three main factors limiting cassava output in Africa: limited market access, insufficient finance, and lack of good quality planting materials for improved varieties. Given that market access is one of the significant constraints limiting cassava production in Nigeria, a more market-driven approach

should be used in developing suitable and acceptable cassava varieties for farmers. The global demand for cassava starch has increased dramatically since 2009, with an annual estimated 2.2% increase that peaked at 6.6 million tons in 2016 (IMARC 2022). The global cassava starch market trade exceeded $40.53 billion in 2018 and it is expected to hit $66.84 billion by the year 2026 (FBI, 2020). Thailand is the leading exporter and earner in the global starch market (Statista, 2023). Unfortunately, Nigeria's share in 2021 was $118.81 million (US dollars), with a projected increase to $198.11 million in 2029 if annual growth of 6.6% is maintained (DBMR, 2020). The industrial cassava value chain in Nigeria is worth $150,000,000 per year and is expected to generate $300,000 in FOREX earnings per day. Ceballos *et al*. (2010) examined the challenge of a large disparity in productivity between Nigeria and Thailand in terms of crop end use and market availability. In countries like Nigeria, where subsistence farming dominates crop production, the crop serves an essential food security role, while in Thailand, the crop is a commercial crop with an eye toward industrial use and immense export potential. The optimization of productivity-related plant architecture and yield traits such as harvest index and dry matter content contributed to the success story in Thailand and south-east Asia (Kawano, 2003). The high yield per hectare obtained in Thailand may be linked to the intense attention paid to cassava production, where it is recognized as a commercial crop due to its enormous export potential. Nigeria can achieve the same feat with cassava by changing farmers' mindsets to embrace commercial cassava production, which requires a significant shift from manual to mechanized cassava production (Sanni, 2019; Isaac, 2021).

Akinngbe (2010) identified limited processing options as one of the factors contributing to low productivity. He suggests the establishment of cottage cassava starch processing hubs could boost cassava production by offering more income and improved capacity to producers, thereby ensuring sustainable production. However, significant investments in cassava processing plants would be a waste of money due to insufficient raw materials to feed the growing population, let alone meet the daily fresh root demands of industrial platforms (Sanni, 2019; BP, 2022). Nigeria has achieved great strides in cassava production; that notwithstanding, the seasonal availability of fresh cassava roots constantly limits the all-year-round functionality of starch processing plants. This challenge was experienced in Brazil and Thailand. It was addressed by developing early maturing, high-yielding cassava varieties with ideal plant architecture for farmers' use (Dufour *et*

al., 1996). Nweke *et al*. (2002) identified four stages that led to the cassava revolution. These stages are described based on the purpose for which the crop is currently deployed, namely deployment as a reserve crop to mitigate the effects of famine (first stage), crop serves as a staple for rural dwellers (second stage), crop gained relevance among urban dwellers and serves as a source of income (third stage), and crop deployed to drive industrial growth (stage four). Given the foregoing, Nigeria's status has shifted from the third to the early stages of the fourth stage. This is characterized by the country's cassava market being segmented into consumer-driven product segments, namely fresh consumption, industrial, and freshly processed food segments. To accelerate industrialization, massive investment in cassava mechanization is required.

While technical solutions for biotic and abiotic constraints are advancing, their impact is nullified by persistent socioeconomic and systemic barriers such as heavy reliance on manual labour, particularly for weeding and seasonal glut and scarcity of cassava roots, which stifles industrial investment and profitability. The adoption of integrated models that simultaneously address the challenge of availability and acceptability of improved cassava planting materials, availability of affordable portable mechanization tools, market linkages, and processing infrastructure would create a synergistic boost for the entire cassava value chain in Nigeria, thereby leading to increase in productivity per unit area.

2.4 Prospects of the cassava starch industry in Nigeria

Cassava starch, one of the products derived from fresh cassava roots is a valuable raw material for the food, beverage, pharmaceuticals, paper, and textile industries. Starch can also be derived from grains such as maize and root crops such as potatoes. However, cassava starch is in high demand based on its superior quality (Holdings, 2018). The process involved in making cassava starch is less cumbersome and cost-effective in comparison to the process involved in obtaining starch from grains (FBI, 2020). Consumer awareness and preference for healthier diets are crucial elements driving a significant shift in eating habits. The increase in cassava starch demand by actors in the food industry might also be linked to consumers being more aware of the health benefits that are associated with the consumption of cassava starch. Some of these advantages include the avoidance of chronic illnesses and the promotion of a healthy lifestyle (FBI, 2020).

Cassava delivers a higher starch quantity per unit of raw material being processed. It has superior starch quality (thickening, taste, texture, purity, paste viscosity, paste clarity, and freeze-thaw stability). These excellent characteristics have positioned cassava starch as a beautiful bride across industries where it serves as an integral component of products like processed foods, beverages, sweeteners, biofuel, MSG/lysine, drilling fluids, modified starch, adhesives, sago pear, textiles, and paper (Holdings, 2018).

Cassava starch is in high demand globally. The global market size of cassava starch in 2018 was valued at $40.53 billion (US dollars), and it is projected to hit $66.84 billion in the year 2026 (FBI, 2020). Nigeria's share in 2021 stood at $118.81 million, and it is projected to reach $198.11 million in 2029 if annual growth of 6.6% is sustained (DBMR, 2020). This implies Nigeria only has access to about 0.29% of the global cassava starch market share despite being the leading producer of the crop globally. Most cassava starch processing companies in the country are currently running at 40% below their installed capacities due to insufficient flow of fresh cassava roots (Sanni, 2019). This calls for the need to address challenges responsible for insufficient fresh cassava roots for industrial use and FOREX earnings. It is imperative to ensure that the production of fresh cassava roots receives robust attention and an aggressive boost to meet the country's rapidly growing demand.

Nigeria is the net importer of starch, ethanol and sweetener. The country imports about 1.7 million metric tons of starch which costs about $26.7 million. At the same time, the country imports $23.3 million worth of sweeteners annually (Adewunmi, 2019). Over $600 million was spent on starch and ethanol importation as of October 2019. The high cost of production of fresh cassava roots, inadequate processing facilities, and inadequate infrastructure all led to low cassava production in Nigeria. In addition to these challenges, intense competition from the fresh cassava consumption and semi-fresh food-centric (staple crop) processing sectors whose two main products are Garri and fufu makes it difficult for industries to have cheap and uninterrupted access to fresh cassava roots. Being the highest producer of fresh cassava roots globally, Nigeria has a competitive edge in maximizing cassava starch production. It also has the potential to double its fresh cassava roots production rate.

Cassava is key to the reduction of food importation bills incurred by African countries, especially Nigeria. Nigeria is significantly dependent on imports from other nations for food and other necessities, which puts a strain on the local currency. Nevertheless, there is a chance to

alleviate this problem through import substitution, particularly by concentrating on cassava and its byproducts like starch, ethanol, and flour. African nations may save $35 billion in food import costs by investing in cassava cultivation and processing. Cassava is an adaptable crop that can grow in diverse environments and be processed into a different types of unique products, providing potential for local industry and lowering the need for imports. Additionally, cassava exhibits resilience to the impact of climate change and provides nutritional security in addition to employment opportunities. Cassava consumption, processing, and farming must be prioritized if food import costs are to be cut (Fregene, 2021).

The demand for fresh cassava roots in Nigeria is increasing gradually and is forecast to quadruple due to population expansion, which is estimated to double by 2050 (United Nations, 2019), and the continuous acceptability and utility of cassava starch as a cheap and healthier substitute to starch sourced from grains and its use as a raw material in numerous sectors is also expanding (Holdings, 2021). In the face of the country's economic challenges, primarily orchestrated by dwindling fortune in forex earning, cassava starch is one of the low-hanging fruits the government can harness to boost its economy through improved forex earning.

The economic potential of the Nigeria's cassava starch industry remain underexploited but its full realization depends on bridging the gap in the production–processing pipeline through targeted investment in the production of fresh cassava roots, improved infrastructure and policy incentives for strong industrial integration and growth, enhanced supply chain linkages and adequate processing capacity.

2.5 Mechanized Industrial Cassava Production

Nigeria's population is growing at a rate of 2.62% per year and is expected to double by 2050 (United Nations, 2019), causing more people to need food. However, food production capacity, particularly cassava, has not significantly increased due to low farmer yields. About 80% of farmers in Nigeria depend on hand tools for crop production, and the country's current mechanization rate is far below the FAO recommendation of 1.5 hp/ha (Mabayoje, 2017). The availability of affordable mechanized devices for key farm management activities and improved cassava varieties is crucial in closing yield gaps and increasing productivity in cassava farmers'

fields in Africa (Sabo *et al*., 2018). In Nigeria, smallholder farmers produce approximately 90% of the country's food crops, but the introduction of technology and the transition to mechanized agriculture is necessary for food security (AGRA 2018; Negrete 2019). Shetty *et al*. (2014) recommended the mass introduction of portable technologies that can boost productivity on farmers' fields. Mabayoje, (2017) opined that cropping intensity must be increased, crop and labor productivity must be optimized, crop and land area under cultivation must be expanded to meet the ever-increasing demand for food and raw materials. Given Nigeria's low or no quota to the cassava export trade, coupled with the rising demand for fresh cassava roots by emerging cassava starch industries and the need to satisfy domestic consumer demands, these seemingly challenges could be managed and turned into drivers pushing the country towards increased productivity through the adoption of mechanized means of cassava cultivation.

Agricultural mechanization has been a game changer in the developed world post-industrial revolution, increasing land productivity, reducing labor demands, alleviating poverty, and ensuring food security (Adams, 2019; Negrete 2019). The issue of low productivity in agriculture has been addressed by agricultural mechanization, which has been successful in other countries like America (Bellis, 2021), China (Huang & Rozelle, 2018) and Europe (Adams, 2019). For example, research shows that in Ethiopia, farmers using combine harvesters can achieve up to 48% higher wheat productivity compared to those using traditional manual methods (Hassena *et al*., 2000). Similarly, in China, every 1% increase in the level of mechanization correlates with approximately a 1.2% increase in crop yields (Peng *et al*., 2022). The mechanization adoption not only raises productivity but also increases farmers' income through more efficient input use and better crop quality. Nigeria has an estimated land mass of 923,768km2, but only 40% of the available agricultural land is cultivated due to the limited capacity of small-holder farmers. Low investment in the mechanized agriculture service market, inconsistent government policy, and resource-limited farmers' inability to access facilities exacerbate the problem . PrOpCom (2009) recommends policy changes and robust investment in the agricultural mechanization service market through public-private partnerships to maximize the use of uncultivated agricultural land for food sufficiency, economic growth, and increased export potential of agricultural commodities. Successful cassava transformation requires improved cassava varieties and mechanical technology-driven innovations to reduce production and processing costs (Nweke, 2005). Some

countries have embraced cassava commercialization for food and industrial use, but Nigeria's potential in this area remains untapped (Kole & Shonnard, 2012).

In Brazil, Vieira *et al*. (2020) identified the Cerrado region in Brazil as a suitable agro-ecological zone with potential for enhanced and sustainable productivity of fresh cassava roots for industrial use. However, yields on farmers' fields were pitiful due to insufficient injection of improved cassava production technology and a lack of improved cassava cultivars developed specifically for the region. To improve the Cerrado region's fortunes, scientists at the Brazil Embrapa Research Institute developed improved cassava varieties that are well-adapted to the target microclimate and have the highest level of quality traits of interest: starch and flour, as well as overall productivity. They also ensured that the developed cultivars have ideal plant architecture, which is essential for ease of crop management through mechanized farming practices (Vieira *et al*., 2018, 2020). A similar approach has been adopted in Nigeria to drive wide adoption of technology in the cassava processing industry in Nigeria. Johnson & Masters (2016) found that a synergy between biological (high-yielding cassava varieties) and mechanical (mechanized cassava processors) technologies increased productivity and growth in the Nigerian cassava industry. The success story of mechanized cassava processing and improved cassava varieties was attributed to the complementarity of innovation theory, which explains the simultaneous mass acceptance and adoption of these technologies. This synergy could trigger a revolution in the cassava starch industry, increasing productivity and quality of fresh cassava roots. Successful design and fabrication of suitable machines for mechanized cassava cultivation, particularly harvesting of fresh cassava roots, will require interdisciplinary collaboration among stakeholders (plant breeders, engineers, and policymakers). Trait modification (plant and root architecture traits) is suggested to develop ideal cassava varieties suitable for mechanized cultivation, which entails modeling the crop into predictable plant architecture and root shape, geometry, depth, and spread of growth in the soil (Kolawole *et al*., 2010). Through this procedure, the positive relationship between plant architecture traits and crop yield would be exploited for increased productivity (Lauri & Lespinasse, 2001; Rymaszewski *et al*., 2017).

In view of the foregoing, the following factors are critical in developing improved cassava varieties that promote increased overall productivity of fresh root yield as well as the quality trait of interest (starch): plant architecture, ease of adoption of modern crop management technology,

and environmental impact. To develop ideal cassava cultivars that promote enhanced and sustainable productivity, it is critical to have a good understanding of these factors. Given that cassava is grown in six different agro-ecologies in Nigeria, it would be important to understand the impacts of the varying environmental conditions on plant architecture and yield (Akinwale *et al*., 2010; Adejuwon & Agundiminegha, 2019).

2.6 Plant Architecture

Plant architecture includes both root and shoot components and their features; crop plants respond to attacks on these features by changing their number and distribution; the nature of the response is largely determined by the growth stage, and the relative position of the plant features being attacked (Room, 1984). The genetic makeup of crop plants determines crop yield, and it has been discovered that some environmental factors, including light, temperature, precipitation, and available soil nutrients, all of which influence overall growth in crop plants and have a direct influence on crop physiological processes, which in turn have a direct influence on crop plant architecture and yield or productivity in the long run (Bailey-Serres *et al*., 2019; Senapati & Semenov, 2020; Hua *et al*., 2022). The possibility of manipulating crop plant branching habits and plant architecture is dependent on available knowledge about the genetic bases of these traits and the ability to predict their effects under varying environmental conditions (Turnbull, 2005; Massetani *et al*., 2011; Costes *et al*., 2013; Andrés & Koskela, 2022). van Esse (2022) emphasized the importance of understanding the genetic bases of yield-architectural traits to design plant varieties with optimized productivity and long-term resilience in the face of changing environmental conditions. Temperature regimes, whether extreme or marginal, play essential roles in shaping crop plants and their architecture (Patel & Franklin, 2009). According to Najla *et al*. (2009), there is a negative correlation between soil salinity levels and tomato plant architecture. Plant architecture breeding has been carried out successfully in important crops like wheat, maize and rice (Fageria *et al*., 2020). With the aid of available genetic information, Sofkova (2008) manipulated the plant architecture of the vegetable bean, *Phaseolus vulgaris*, to convert indeterminate varieties to upright types that are suitable for mechanized farming.

de Reffye *et al*. (1988) used programming software to create plant architectural models that depict plant developmental and growth phases, as well as in silco simulations of environmental

effects such as pest attack, nutrient requirement, and the spatio-temporal evolution of crop plants at different ontological stages. Godin *et al*. (1999) followed up on this by introducing an advanced model (MTG) that incorporates topological and geometrical data into software (AMAPmod) for accurate digitized plant architecture modeling and analysis. This software was successfully used in the modeling and analysis of plant architecture in an apple tree (Godin *et al*., 1999).

With the availability of plant architecture descriptive concepts and analytic models, it is now possible to obtain accurate information on the genetic bases of plant architecture and its manipulation in developing crops with ideal plant architecture (Barthélémy & Caraglio, 2007). Conn *et al*. (2017) investigated the likelihood of having a plant branch in a specific space at any growth stage and under known environmental conditions, regardless of crop species, using 3D imagery. The authors used a statistical procedure with the help of a spatial density function to categorize plant architecture into two types of branch densities: separable and self-similar.

Durai Prabhakaran *et al*. (2019) emphasized the importance of phytomimetics in the successful application of biological data and environmental influence in the development of new crop varieties with optimized plant architecture. Phytomimetics is a subfield of biomimetics that entails the art of learning from nature and using it to one's advantage by mimicking natural outplay. Plant developmental processes such as phyllotaxis, meristem determinacy, apical dominance, and differential growth of stems and lateral organs all contribute to the overall structure or form of the plant. These processes are regulated by various hormones that are activated by specific gene functions; therefore, a thorough understanding of the interplay between gene functions and the growth hormones they regulate would be critical in understanding the genetic bases of plant architecture and its manipulation (Reinhardt & Kuhlemeier, 2002).

The genetic analysis of the relationship between plant architecture traits in rapeseed has been made possible by the discovery of some important loci (Cai *et al*., 2016; Li *et al*., 2016; Li *et al*., 2019), hexaploid wheat (Muhammad *et al*., 2021), oilseed rape (Yang *et al*., 2021), tea plant (Xia *et al*., 2021), and Soybean (Yang *et al*., 2021). Yano *et al*. (2019) isolated an important plant architecture mediating gene *SPINDLY* gene in rice using GWAS, whereas Zhao *et al*. (2015) reported functional analysis of the *PLANTARCHITECTURE AND YIELD 1* (*PAY1*) gene and its introgression into elite rice varieties, which resulted in a 38% increase in grain yield.
Grain yield was also increased by regulating the under-expression of OsPIN5b genes, which resulted in an increase in the number of tillers, underground vigor, and panicle length (Lu *et al*.,

2015) and the loss of function of *INTERACTING PROTEIN1* (*IPI1*), which was characterized by an increase in the number of tillers and enlarged panicles (Wang *et al*., 2017). *TFL1*, the shoot meristem identity gene, also controls plant architecture by regulating the activities of the floral meristem identity genes *LEAFY* and *APETALA 1* (Ratcliffe *et al*., 1998). With the aid of a thorough understanding of the genetic bases of these traits, Dong *et al*. (2021) decided to exploit the potential of a pleiotropic, programmed cell death gene (*OsPDCD5*) in improving yield in rice through the optimization of plant architecture. The authors used CRISPR/Cas9 gene editing to induce gene function loss in *OsPDCD5*. The findings revealed the possibility of increasing crop productivity by manipulating plant architecture. Liu *et al*. (2011) discovered the genetic bases of evolution in the plant architecture of Brassicaceae crop species. The authors attribute the change in crop plant architecture to changes in the genetic sequences of one of the genes that collectively function in controlling shoot and flower disposition, *LEAFY* (*LFY*). As a result of the genetic alterations, there was ineffective repression of the floral meristem identity gene *LEAFY* (*LFY*) by the shoot meristem identity gene *TERMINAL FLOWER1* (*TFL1*), thereby resulting in modified plant architecture. The manipulation of the expression of the *FLOWERING LOCUS T* (*FT*) gene in cotton could promote flowering and reduce indeterminate and vegetative growth, thereby enhancing the productivity of the cotton crop through modified plant architecture (Mcgarry & Ayre, 2005).

2.6.1 Meristem Determinacy and Branching

Two important genes *TERMINAL FLOWER1* (*TFL1*) and *SHOOTMERISTEMLESS* (*STM*) are involved in determining the fate of stem cell whether it remains undifferentiated (meristematic) or differentiates into a specific organ such as leaf or branch. *TFL1* promotes floral meristem identity, while *STM* maintains shoot meristem identity and inhibits flowering. A balance between vegetative growth and reproductive development, and influence on branching pattern is a function of the level of interplay that exists between these two genes and their downstream targets (Jiang *et al*., 2015; Aggarwal *et al*., 2020). In addition to these, the growth potential of the trunk diameter and the level of branching in woody plants are determined by the activities of the genes that regulate the fate of stem cells (Jiang *et al*., 2015; Aggarwal *et al*., 2020).

2.6.2 Hormonal Regulation of Plant Architecture:

Plant hormones play vital roles in terms of the ability of plants to respond and adapt to changes in their environment. These processes lead to modification in growth habit and developmental pattern which modifies the plant architecture. Five major plant hormones have been identified in this regard: auxins, cytokinins, gibberellins, abscisic acid, and ethylene (Wang & Irving, 2011). Each of these hormones has distinct functions and a combination of effects due to their interactions. Auxins are involved in the regulation of lateral bud development, apical dominance and tropic responses in plant which include the control of cell elongation during phototropism and gravitropism (Aloni *et al*., 2006; Gallavotti, 2013; Wakeman & Bennett, 2023). Cytokinins regulate the activities of shoot apical meristem as well as the delay of senescence in leaf tissues and inflorescence architecture. They also promote cell division and regulate several developmental processes in plants (Aloni *et al*., 2006; Han *et al*., 2014; Wu *et al*., 2021). Gibberellins control shoot elongation, root development, seed germination, fruit and flower maturation, seed dormancy, gender expression, and the delay of senescence in leaves and fruit (Liang *et al*., 2014; Castro-Camba *et al*., 2022; Shtin *et al*., 2022). Abscisic acid (ABA) plays conspicuous roles in the regulation of plants' responses to stress, and inhibition of cell division (Harris, 2015; Crespel *et al*., 2022; Friero *et al*., 2022). Ethylene is an important hormone with respect to its role in conditioning fruit ripening. It is also an important component of the growth media in tissue culture as it is used to engender distinct developmental pathways (Schaller, 2012; Chang, 2016; Iqbal *et al*., 2017).

Significant interactions between these hormones have resulted in the modification of plant architecture. For instance, auxins and cytokinins interact to regulate apical dominance, lateral bud development, and tropic responses in plants as well as root elongation and root development (Reinhardt & Kuhlemeier, 2002; Aloni *et al*., 2006; Cui *et al*., 2010; Li *et al*., 2014; Rivas *et al*., 2022).

2.6.3 Transcriptional Regulation of Plant Architecture:

The roles of transcription factors in shaping plant architecture cannot be overemphasized. The expression of genes that are involved in key pathways that determine the architecture in plants such as cell division, elongation and differentiation are being regulated by transcription factors (Nicolas & Cubas, 2016; He *et al*., 2020; Berry & Argueso, 2022; Lu *et al*., 2022). They also

moderate the process of organ development and overall morphology of plant (Heisler *et al*., 2022). Prominent among the transcription factors that influence the processes that shape plant architecture are members of these families of transcription factors *MYB*, *bHLH*, and *WRKY*.

The members of the *MYB* family of transcription factors have played important roles in conditioning plants for successful adaptation to a multitude of environments (Chang *et al*., 2020), regulation of root growth in plants (Chen *et al*., 2022), modulation of biotic and abiotic stress reactions in plants (Ambawat *et al*., 2013), and control over secondary metabolic pathways in plants (Cao *et al*., 2020). Likewise, the *Basic Helix-Loop-Helix* (*bHLH*) family members play a critical role in controlling plant growth, development, and response to abiotic stress (Zuo *et al*., 2023), and enhancing the tolerance of plants to abiotic stress (Guo *et al*., 2021; Qian *et al*., 2021; Xue *et al*., 2023). The members of *WRKY* transcription factor family are involved in the regulation of tillering and panicle branching (Duan *et al*., 2019), as well as tiller angle and plant architecture (Ding *et al*., 2021) in rice.

2.6.4 Plant Architecture, Mechanized Farming, and Crop Yield

Some plant architecture traits such as plant height, branching habit and canopy cover are important determinants of crop yield. Likewise, these traits are equally important in determining the suitability of crop plants for mechanized cultivation (Mathan *et al*., 2016; Murchie & Burgess, 2022). The relationship between plant architecture and mechanized farming practices significantly influences crop yield (Yan *et al*., 2019). Improved levels of productivity and efficient use of resources could be attained on farmers' fields through the optimization of plant architecture for mechanized cultivation (Mathan *et al*., 2016). To achieve the intended level of sustainable productivity, the levels of tradeoffs that must be tolerated must be balanced (Coyne, 1980).

A great deal of work has been done in simulating crop productivity using crop modelling techniques supported by machine learning algorithms (van Klompenburg *et al*., 2020; Muruganantham *et al*., 2022)

Much progress have been made with crop models in unravelling the contributions of plant architecture traits to productivity in crop plants but little is known about the link between the genetic composition of the plant and the differential performance observed in the productivity levels realized through in silico simulations (Boote *et al*., 2021). The introduction of the functional-structural components into the crop simulation models has paved the way for significant headways

in terms of understanding the effect of the relationship between crop growth and plant architecture on the overall crop productivity (Letort *et al*., 2008; Guo *et al*., 2011).

2.6.4.1 Plant Architecture in the Machine Age:

At the onset of crop domestication, crop varieties were naturally selected for human-powered cultivation which placed much emphasis on traits that encourages the ease of manual cultivation, management, harvesting and post-harvest handling of crop plants (Reid, 2011; LABS, 2023). However, the injection and rising dominance of mechanization in agriculture has mandated a shift from the traditional breeding themes to more sustainable, market and productivity-driven breeding plans (Reid, 2011).

2.6.4.2 Key plant architectural traits influencing mechanized farming include:

Plant height: Tall plants are prone to lodging and this creates challenges for farmers who intend to deploy mechanized harvesters, thereby leading to yield losses from grain shattering and increased operational costs. Shorter, stiffer varieties with strong stems provide solutions to these challenges (Shah *et al*., 2019).

Stem strength: Imbalance in weight distribution along the shoot, root and totality of a plant predisposes the plant to lodging risk. Stem strength is a function of the stem diameter, as well as the stem wall (Bisht *et al*., 2022). This makes stem diameter an important trait that determines crop productivity and its suitability for mechanized cultivation.

Branching patterns and canopy architecture: Intensive branching pattern can impede easy movement of machineries across the field thereby making mechanized cultivation tedious and unproductive (Nakamasu & Higaki, 2019). Meanwhile, plants with open canopies with evenly spaced branches would promote hitch free mechanical operations and efficient light interception (Burgess *et al*., 2016; Mediavilla & Escudero, 2023).

With reference to cassava, some important plant architecture traits that determine its suitability for mechanized cultivation and enhanced productivity have been identified. The optimization of these traits (plant height, height at first branch, harvest index, stem diameter, branching habit, angle of branching and lodging resistance) will promote compatibility of the crop for mechanized cultivation and increased productivity (Chalachai *et al*., 2013; Ceballos *et al*., 2020; de Oliveira *et al*., 2020).

2.6.5 Cassava Growth Habit

Cassava is grown throughout the tropical regions and in some parts of the Pacific. This is because of the crop's remarkable adaptability and adaptable growth pattern.

Cassava is monoecious, with flowers on terminal panicles. Male and female flowers grow on each panicle. Flowering is influenced by branching level, so erect; unbranched plants perform worse in terms of flower production than branched plants (Jennings & Iglesias, 2018). Due to its protogynous nature, female cassava flowers emerge ten days before the male flowers on the same inflorescence. Cassava is a cross-pollinated crop, and the primary pollinators are insects.

Occasionally, when male and female flowers emerge simultaneously on different branches, self-pollination can occur. Cassava is classified as a C_3 crop due to its photosynthetic mechanism. The leaves are alternate, with three to nine lobes and palmated veins.

A mature cassava stem is woody, with protuberant leaf scars at the nodes. The main stems can remain intact or divide to form different branching habits, such as dichotomous, trichotomous, or tetrachotomous (Fukuda *et al.*, 1998; Lebot, 2019).

The level of branching is determined by the number of flowering events which transforms the shoot apex to flowering buds. The manner of branching determines plant architecture; some varieties produce branches at the base, while others remain upright for most of the growth phase and branch at the apex. Cassava roots are the crop's primary storage organ. Plants propagated by seed produce tap roots, which develop into fibrous roots, whereas plants propagated by stem cuttings produce adventitious roots from the base of the cuttings, which eventually form a fibrous root system. Some of the fibrous roots develop into tubers, while the remainder function in soil nutrient adsorption. The cassava roots are linked to the shoot by a neck located at the base of the shoot (Lebot, 2019).

Cock *et al.* (1979) developed a cassava growth model through a computer simulation program. The model revealed a vital relationship between increased yield and lateness in branching, large-sized leaves, and long shelf life of leaves. Ramanujami (1984) on the other hand, coined the term "Harvesting Efficiency" to describe the coefficient of assimilate partitioning in terms of the percentage of dry matter partitioned to the cassava root per unit of dry matter synthesized by the plant. Based on the foregoing, the author concluded that: varieties with few or no branches have significantly higher harvesting efficiency than varieties with a prolific branching habit. Irikura *et al.* (1979) reported a combination of direct and inverse relationships between leaf

area index and dry matter content; initially, dry matter content increased progressively with increasing leaf area index until a specific value of leaf area index (3) was reached, at which point the dry matter content began to decrease despite increasing leaf area index values. The authors discovered that the environment had no effect on the relationship.

Zhou *et al*. (2020) discovered a link between amylose content and branching in fresh cassava roots. The authors confirmed that silencing cassava branching genes increased amylose content in fresh cassava roots. Fakir *et al*. (2011), on the other hand, concluded that an increase in the magnitude of debranching was responsible for the decrease in root yield. This was consistent with the findings of Lian & Cock (1979), who investigated the relationship between branching habit and yield. According to the authors, cassava roots can absorb more assimilate than usual. Hence, attaining a balance in assimilate partitioning between sink and source is crucial. The authors concluded that this balance was best achieved among late branching genotypes, thereby responsible for their higher yields compared to early branching genotypes. Similarly, Cock (1976) expressed the same sentiment regarding the need to strike an optimal balance between assimilate partitioning and yield maximization. The author, on the other hand, emphasized the importance of harvest index to yield maximization. El-Sharkawy & De Tafur (2010) discovered that the tall plant type produced higher storage root yield in a comparative study between two cassava plant types: tall plant type with large leaf canopy and shoot biomass and short plant type with typical small leaf canopy and shoot biomass. However, the short plant type used nutrients more efficiently than the tall plant type. While comparing different branching habits in cassava and their effects on yield, Jennings & Iglesias (2018) concluded that plants that branch early and frequently after planting produce high dry matter content but distribute very little to the roots, limiting root yield. Tall plants with higher branching, on the other hand, were not exceptional in terms of root yield, but plants that branched at about one meter above ground with moderate branches were found to be suitable and desirable for root yield optimization. According to Hershey (2003), an erect plant type with a medium to late branching habit is suitable for effective crop management. He also mentioned that erect plant architecture ensures the availability of suitable cuttings for planting. However, pruning of cassava branches at every three months' interval, starting from three months after planting to twelve months after planting, led to a 40-80% reduction in fresh root yield and a significant decline in starch contents (Adjebeng-Danqua & Safo-Kantanka, 2015).

Plant height is one of the important plant architecture traits that influence crop yield and productivity. Mora Moreno *et al*. (2016) used a mapping population obtained from one hundred and thirty-three full-sib F_1 cassava genotypes to identify significant QTLs that are responsible for productivity, plant height, number of shoots, and length of internode in cassava. To reveal and exploit the genetic potential of some recessive alleles in the cassava germplasm, a couple of cassava accessions were selfed, and their progenies were carefully examined. A particular progeny with erect plant architecture within the first six to eight months of planting was identified. The progeny also lacked leaf petioles (Ceballos *et al*., 2010). The authors pointed out that genetic gains in productivity is highly correlated with the modification of plant architecture. Hence, plants with this unique architecture have a massive potential for commercial use in terms of foliage harvesting, improved productivity through increased planting population to about 30,000 plants ha^{-1}, and mechanized cultivation.

Significant progress has been made in understanding the influence of genetic, hormonal and environmental factors on plant architecture, however, a direct link between these factors and the modification of the architecture of crop plants for suitability to mechanized cultivation and optimization of yield, particularly in cassava, is still lacking. A good understanding of the genetic characterization of cassava plants with favourable architecture for mechanized cultivation would aid the development of suitable cassava varieties with enhanced productivity.

2.7 Molecular Markers in Cassava Breeding

The application of molecular markers for cassava breeding dates back to Marmey *et al*. (1993). The first set of markers used in genetic diversity studies are random amplified polymorphism (RAPDs) and restriction length polymorphism (RFLPs) markers. These were followed by amplified fragment length polymorphism (AFLPs) makers prior to the introduction of single sequence repeat (SSR) markers. Ferreira *et al*. (2008) utilized Random Amplified Polymmorphic DNA (RAPD) markers in dissecting genetic diversity amongst yellow-orange root cassava accessions while Adjebeng-Danquah *et al*. (2020b) used simple sequence repeat. Following the challenges bordering on marker density and cost effectiveness, new marker technology; Diversity Array Technology (DArT) was introduced. It is a micro-array DNA hybridization-based technology. It was first used for genetic studies in cassava in the year 2005. It guarantees, wider genome coverage, high throughput, robustness, cost effectiveness and ease of

applicability (Xia *et al*., 2005; Ferguson *et al*., 2012). Diversity Array Technology has been useful in unravelling genetic diversity among cassava accessions (Adu *et al*., 2020a). Although, SSR markers displayed higher differentiation potential when compared with DArT but DArT was preferred based on its high throughput and suitability for use on cassava; a seemingly orphan crop with limited alternatives (Hurtado *et al*., 2008). Xia *et al*. (2005) claimed that the DArT marker system possesses a competitive edge over other marker technology systems used in cassava genotyping in terms of cost effectiveness, ease of marker recovery and analysis. DArT was also applied in improving the carotenoid contents of cassava accessions through genomic selection (Esuma *et al*., 2021). DArT was also instrumental in the diversity study, germplasm conservation and preservation of virus free local genetic resource (Adu *et al*., 2021; Ferguson *et al*., 2021; Pierre, 2021; Orek *et al*., 2022).

2.8 High Throughput Phenotyping Protocols

With the drastic reduction made to the cost of genotyping and its accuracy, the possibility of handling a robust breeding population per time has been made feasible. This has opened doors to a greater challenge with respect to ease of phenotyping the overwhelmingly large breeding population. Conventional phenotyping approach used in estimating yield and key traits, including starch, carotenoid and dry matter content has been associated with drudgery, high cost, low throughput, and human error. To complement the gains associated with the high throughput and cost-effective genotyping protocols, there is urgent need to develop more vibrant, cost-effective and precise phenotyping protocols to accelerate progress in cassava breeding. High-throughput phenotyping approaches such as Normalized Difference Vegetation Index (NDVI) and Near-infrared Reflectance Spectroscopy (NIRS) would enhance the possibility of obtaining consistent and reliable phenotype data.

2.8.1 Near-Infrared Reflectance Spectroscopy (NIRS)

Near-infrared Reflectance Spectroscopy (NIRS) is an analytical technique that determines the chemical composition and physical properties of a sample based on its interaction with near-infrared light. The principle underlying the application of NIRs is that different molecules absorb light at certain wavelengths, and this gives rise to unique spectral fingerprints. NIRS uses a light source that emits radiation in the near-infrared range, typically between visible light (780 nm) and the mid-infrared region (2500 nm) (Osibanjo *et al*., 2013; Beć *et al*., 2020; Kinhal, 2022).

Molecules vibrate and rotate at specific frequencies. When NIRS light interacts with a sample, certain molecules absorb specific wavelengths of NIRS light corresponding to their vibrational and rotational energy levels. This unique pattern of absorption and reflection of each molecule at different wavelengths constistutes its spectral fingerprint. By analyzing the spectrum of NIRS light that passes through or is reflected from a sample, we can identify and quantify the chemical composition and physical properties in the sample (Osibanjo *et al*., 2013; Beć *et al*., 2020). NIRS offers a rapid, non-destructive, and cost-effective phenotyping protocol for estimating essential crop traits, thereby aiding their improvement through accurate and accelerated selection (Kinhal, 2022).

Near-infrared Reflectance Spectroscopy (NIRS) technology has been evaluated for several purposes, including quantification of nutrient contents in food crops (grains, roots, and tubers), (Montes *et al*., 2013; García-sánchez, 2015; Johnson & Walsh, 2020), assessing dry matter content and cyanogenic potential (Sánchez et al., 2014), starch content (Maraphum, Saengprachatanarug, & Wongpichet, 2020), beta carotene and total carotenoid content in cassava (Ikeogu *et al*., 2019) as well as estimating texture and cooking time of common beans (Wafula *et al*., 2020). This technology has also been used in in-vivo estimation of chlorophyll contents in leaves (Li *et al*., 2019). NIRS has also been used in selecting rice seed mutants from a seed lot exposed to mutagenic treatments (Jankowicz-Cieslak *et al*., 2016).

2.8.2 Normalized Difference Vegetation Index (NDVI)

Multispectral image data obtained through Unmanned Aerial Vehicle and satellite imaging have been widely used in predicting yield and overall fitness of crop plants. However, these devices are quite expensive and could not be deployed in low-budget phenotyping evaluation. One of the most important data obtained through these protocols is the Normalized Difference Vegetation Index (NDVI). NDVI works based on the relationship between reflected and absorbed light in the red and near infrared bands.

$$\text{NDVI} = \frac{(NIR-Red)}{(NIR+Red)}$$

NIR- Near infrared band

Red – Red band

The approach has been successfully deployed in precision agricultural practice with respect to determining the exact fertilizer need per plot in a massive crop plantation and in unravelling the incidence and severity of disease and capturing of adequate scoring data. The use of NDVI data has also been deployed in predicting yield of crop plants at different phenological stages. Mirasi *et al*. (2021) deployed NDVI and four other vegetation index data in predicting grain yield in wheat. The authors observed that the NDVI-based model gave the most accurate result and the best growth stages of yield estimation were milking and maturity growth stages. Vannoppen & Gobin (2021) outlined the lack of sensitivity of the NDVI data to environmental factors as a source of its weak accuracy in predicting yield in winter wheat. The authors observed more accurate prediction with precipitation and temperature data at the tillering and anthesis growth stages of the crop. This agreed with the findings of (Rasmussen, 1998).

Jiang *et al*. (2003) observed a trend between NDVI data and developmental stages in winter wheat, the authors also established a relationship between grain yield and NDVI data, hence, they proposed the use of these data in the prediction of both yield and crop phenology. Meanwhile, Moriondo *et al*. (2007) deployed a cropping system simulation model aided by NDVI data in getting an accurate estimation of wheat yield. Mkhabela *et al*. (2011) affirmed that the accuracy of crop yield prediction through the NDVI data is influenced by the crop type, time of the growing season and agroecological zone.

The use of the NDVI data extracted from multispectral sensors mounted on unmanned aerial vehicles have been instrumental for accurate yield prediction and most reliable phenological stage for prediction, which is silking stage in maize, Sanodiya *et al*. (2017), early reproductive and late ripening stages in rice and middle reproductive to early ripening stages in wheat (Guan *et al*., 2019). Sanodiya *et al*. (2017) integrated the chlorophyl content data obtained through the N-Tester in their NDVI data analysis while Guan *et al*. (2019) established a correlation between NDVI information and fertilizer application rates in both rice and wheat. Also, Aranguren *et al*. (2020) demonstrated the effect of nitrogen deficiency levels on grain yield in wheat using NDVI data. Selvaraj *et al*. (2020) developed image analytic tool (ICIAT Pheno-i) that facilitated the processing of remotely sourced multispectral image data for yield prediction in cassava while Purnamasari *et al*. (2019) deployed aerially generated multispectral data for both yield prediction and selection of suitable crop land for optimum productivity in cassava.

2.9 Important Statistical Methods in Cassava Breeding

2.9.1 Importance of Genotype by Environment Interaction (GxE) and Stability Analysis in Cassava Breeding

Genotype by environment interaction (GxE) and stability analysis are essential statistical tools deployed by plant breeders to identify genotypes that perform excellently across diverse and changing environments (Begna, 2020). These analyses enable the selection of genotypes with consistent and high performance, thereby increasing the efficiency and effectiveness of breeding programs. Genotype by environment interaction (GxE) and stability analysis are quite important in cassava breeding due to the crop's wide adaptation to diverse environmental conditions and the significant variability in the expression of its traits across agroecologies (Begna, 2022).

GxE interaction echoes the differential performance of genotypes under varying environmental conditions which complicates the process of selecting superior and stable genotypes for crop improvement. This is well pronounced in cassava where GxE interaction affects important yield and plant architecture traits such as fresh root yield, dry matter content, shoot yield and resistance to biotic stresses like cassava green mite (Amelework *et al*., 2023; Filho *et al*., 2024; Jiwuba *et al*., 2020). Accurate assessment of GxE enables breeders to target genotypes to specific environments and or discover stable genotypes that perform well across diverse conditions, improve genetic gains and ensures successful delivery and release of improved crop variety (Amelework *et al*., 2023; Filho *et al*., 2024).

Hence, it is imperative to explicitly understand and quantify GxE in the breeding population to exploit genetic variability and achieve reliable breeding outcomes for specific target environments or broader adaptation. Studies show that in most cases, the proportion of phenotypic variance explained by GxE in cassava is higher than genotypic variance for important traits like fresh root yield. This indicates that genotypes differ in their responses across environments and that a superior genotype in one environment may not record similar performance in another environment (Amelework *et al*., 2023; Filho *et al*., 2024; Jiwuba *et al*., 2020).

Additive main effects and multiplicative interaction (AMMI) and genotype main effect plus genotype x environment (GGE) biplot models have been widely used to dissect GxE and identify genotypes with broad or specific adaptation through stability analysis (Agyeman *et al*.,

2015; Amelework *et al*., 2023; Bilate Daemo *et al*., 2023). Stability analysis complements GxE studies by identifying genotypes that maintain consistent performance across different environments, reflecting adaptability and resilience. It helps breeders select genotypes that combine high yield potential with environmental stability, essential for sustainable crop production under diverse conditions (Amelework *et al*., 2023; Filho *et al*., 2024; Jiwuba *et al*., 2020).

2.9.1.1 Practical Implications

GxE and stability analyses help breeders in developing varieties that are adapted to the specific agro-ecologies, increased yield reliability and end users' acceptability. They pave the way for the identification of mega-environments that epitomize the cluster of environments that depict consistent performance of genotypes, thus optimizing resource allocation in breeding trials. Stability analysis supports decision-making by balancing yield potential with risk reduction, ensuring sustainable production of fresh cassava roots especially under changing climatic conditions.

Genotype x environment interaction and stability analysis are indispensable statistical tools in modern day plant breeding. They improve the accuracy of genotype selection by revealing how genetic expression is modulated by environmental factors and by identifying genotypes with robust performance thereby contributing to the improvement of the yield of fresh cassava roots and food security (Adham *et al*., 2022).

2.9.2 Importance of Path Coefficient Analysis in Cassava Breeding

Path coefficient analysis is an important statistical tool that partitions correlation coefficients between traits into direct and indirect effects. Path coefficient analysis relies on well-designed replicated experiments and accurate estimation of variances, covariances, and correlation coefficients. It provides a biologically interpretable framework by expressing direct and indirect effects as standardized partial regression coefficients. This ability to decompose effects statistically is critical in polygenic traits where multiple interrelated traits influence the target outcomes (Randolph & Myers, 2013). This further decomposition of the correlation coefficients helps breeders understand the nature and strength of causal relationships between traits thereby facilitating more informed selection decisions for crop improvement (Diniz & de Oliveira, 2019).

Cassava yield is influenced by a couple of interrelated morphological, agronomic and root quality traits. Path coefficient analysis helps clarify these interrelationships and identifies which traits have

the most substantial direct effects on yield. Studies have shown that traits such as root diameter, number of roots per plant, plant height, shoot weight, and aboveground biomass have meaningful direct and indirect effects on fresh root yield and starch yield in cassava (de Oliveira *et al*., 2021; Njoku & Mbah, 2020). This technique enables breeders to focus selection on traits that will effectively increase cassava root yield through indirect selection, especially when traits with low heritability can be improved via selection on correlated secondary traits with higher heritability. This strategic trait prioritization accelerates genetic gain and efficiency in breeding programs (Diniz & de Oliveira, 2019).

Studies revealed root diameter often exhibits the highest positive direct effect on fresh root weight, making it an important target for selection in cassava improvement (de Oliveira *et al*., 2021; Njoku & Mbah, 2020) while traits like plant height and number of roots per plant present negative and possitive direct effects respectively but contribute positively to yield through indirect pathways (de Oliveira *et al*., 2021; Njoku & Mbah, 2020). Path analysis in cassava reveals high residual effects in some cases, thereby suggesting additional yield components or traits may still need consideration for a better understanding of yield determinants (Daemo *et al*., 2022; Kundy *et al*., 2014).

2.9.2.1 Applications and Benefits

Path coefficient analysis aids in prioritization of traits for indirect selection: Selecting for root diameter, shoot weight, and number of roots per plant can result in better gains for fresh root yield than direct selection alone (Diniz & de Oliveira, 2019). Path analysis helps the breeder to sequentially examine complex causal relationships, hence avoiding misleading conclusions based on the output of the correlation analysis alone (Limbu, 2021; Mahalakshmi *et al*., 2024). By identifying traits with higher heritability and strong direct effects on yield, breeders can optimize selection accuracy and speed (Diniz & de Oliveira, 2019). Path diagrams and effect estimates assist in developing effective breeding schemes and deciding on key phenotyping traits to measure (Rosa *et al*., 2011).

Path coefficient analysis is an essential analytical tool for cassava breeding. It advances understanding of the genetic and physiological basis of yield and related traits by separating direct from indirect effects. This helps breeders choose the most impactful traits to improve, optimize breeding selection criteria and ultimately increase root yield and starch content. Its application in

cassava breeding programs enhances the efficiency, precision and success of genetic improvement efforts (Daemo *et al.*, 2022; Diniz & de Oliveira, 2019; Yeshitila *et al*., 2023).

CHAPTER THREE

3.0 GENETIC DISSECTION OF PLANT ARCHITECTURE AND YIELD-RELATED TRAITS IN CASSAVA USING GENOME-WIDE ASSOCIATION ANALYSIS

3.1 Introduction

Cassava (*Manihot esculenta* Crantz), is the sixth most crucial food crop globally, it is cultivated for its starchy tuber which is a primary food source and industrial raw material (FAO, 2020a; OWID, 2021; UNdata, 2021). With an estimated 315 million tonnes of fresh cassava roots harvested in 2021, it is a staple food for around 800 million people worldwide, primarily in Africa, Asia, and Latin America (FAO, 2020a; OWID, 2021; UNdata, 2021). Cassava is Africa's second most important food crop after maize, accounting for over 65% of the world's production of fresh cassava roots (FAO, 2020a). The crop is a cheap source of dietary carbohydrate and calories for over 40% of Africa's population, especially in forest and transition zones (Alves, 2002; Nweke, 2004; FAO, 2020a). Cassava starch, derived from fresh cassava roots, has widespread applications in various industries, including food, feed, textile, paper, pharmaceutical, cosmetic, biofuel, and bioplastics (Li *et al*., 2017). The global demand for starch-based products is intensifying the pressure on cassava productivity, and enhancing cassava productivity is crucial to meet this demand (Kaur & Ahluwalia, 2017; Chisenga *et al*., 2019).

Under ideal conditions, cassava can produce up to 90 tons of fresh roots per hectare, equivalent to 27 tons of dry matter per hectare (El-sharkawy, 2004; FAO, 2021). One way to boost the yield potential of crop plants, especially cassava is through plant architecture (Lauri & Lespinasse, 2001; Rymaszewski *et al*., 2017; Mansaray *et al*., 2020). Plant architecture encompasses the way plant organs like stems, leaves, branches, and roots are spatially configured and arranged. It wields a crucial influence over the growth, development, and yield of crops, impacting vital factors like light interception, photosynthesis, water-use efficiency, nutrient absorption, pest and disease resistance, and the crop's harvest index (Mathan *et al*., 2016; Murchie & Burgess, 2022).

In addition to plant architecture, prospects of mechanized cultivation and harvesting can also boost cassava yield potential. Mechanized cultivation and harvesting can reduce labour costs, increase

efficiency, and improve the quality of cassava products (Patiño *et al*., 2002; FAO, 2013). Developing cassava varieties suitable for mechanized production and harvesting requires the introgression of specific characteristics such as uniform root size and shape, straight stem, shallow root attachment, high yield potential, disease resistance, and adaptability to different environments (Patiño *et al*., 2002; Kolawole *et al*., 2010; Sike-Ezo, 2021).

Different crops may have specific optimal plant architectures for maximizing yield potential under different conditions. For instance, high-yielding rice varieties possess moderate plant height and an increased number of tillers, while enhanced maize productivity results from manipulation for increased plant height, leaf angle, and branching (Mathan *et al*., 2016). In the case of cotton, plants with heights in the range of 80-120 cm and an increased number of fruiting branches are recommended for optimal yield and mechanized harvesting (Yan *et al*., 2019). Agronomic traits related to plant architecture, including plant height, branching pattern, and canopy characteristics, significantly impact crop yield (Mathan *et al*., 2016). It was reported by Mansaray *et al*., (2020) that plant height, stem diameter, and canopy width all had a significant impact on cassava yield. Plant height has played critical roles in regulating the morphogenesis of crops such as rice and wheat, as well as their capacity to withstand lodging and intercept light for photosynthesis, all of which led to greater grain yield. However, both genetic and environmental differences impact the appropriate plant height for maximum productivity (Yu *et al*., 2020; Zhang *et al*., 2017). In cassava, Okogbenin & Fregene (2003) discovered significant phenotypic relationships between plant height, height at first branch, and fresh root yield. Meanwhile, El-Sharkawy & De Tafur (2010) concluded that short to medium stemmed cassava plants displayed more impressive nutrient-use efficiency and increased productivity compared to taller plants, thereby recommending this feature for cassava improvement. The optimal plant height for mechanical cultivation in Brazil, according to research by Oliveira *et al*. (2020), is 2.29 meters, with a height of 1.60 meters at the first branch. A balance between increased yield and ease of harvesting was achieved at these heights. Cassava production is labour-intensive and costly, but mechanization can improve its productivity and efficiency. However, mechanization is not widely adopted in Africa and other regions, mainly due to the technical challenges posed by cassava's complex plant architecture and diverse root morphology (Ospina *et al*., 2002; Patiño *et al*., 2002; Chalachai *et al*., 2013; Ikuemonisan *et al*., 2020).

Cock *et al*. (1979), developed a computer-based simulation model that predicts an ideal plant type for maximum yield under favorable growth conditions. According to him, an ideal cassava plant that guarantees maximum yield must have the following features: produce branches at an advanced growth stage to give room for the formation of more leaves per plant, possess large leaves which increases leaf area index, has long leaf life, produce at least nine roots per plant. Crop plants with an ideal plant architecture can indeed produce maximum yield while also being suitable for mechanized cultivation and harvesting (Hedden, 2003; Yan *et al*., 2019; Oliveira *et al*., 2020). According to Bailey-Serres *et al*. (2019), genetic strategies for improving crop yields, entails the following: enhancing photosynthesis efficiency, optimizing nutrient and water use efficiency, increasing stress tolerance and resilience, and modifying plant architecture. He opined that these strategies would help plants grow better in nutrient-poor or water-limited environments, improve stress tolerance and resilience, and optimize planting density, light interception, and mechanical harvesting.

The genetic regulation of plant architecture is complex and involves multiple genes and a combination of factors, including miRNAs, transcription factors, hormone homeostasis, and signalling pathways (Wang & Li, 2006; Mathan *et al*., 2016; Guo *et al*., 2020). Several studies have attempted to dissect the genetic basis of plant architecture traits and their effects on cassava yield using quantitative trait loci (QTL) mapping (Okogbenin & Fregene, 2003; Mora Moreno *et al*., 2016; Srisawad *et al*., 2023). Understanding the mechanisms and manipulation of plant architecture is a key challenge and opportunity for cassava improvement.

Significant progress has been made through the deployment of genome-wide association studies (GWAS) in unravelling the genetic underpinnings of a number of important traits in cassava such as carotenoid content (Esuma *et al*., 2016; Ikeogu *et al*., 2019), geomorphological and quality-related traits (Rabbi *et al*., 2022), resistance to cassava root rot (Brito *et al*., 2017), drought tolerance (dos Santos Silva *et al*., 2021), resistance to cassava mosaic disease (Wolfe *et al*., 2016) and root mealiness (Uchendu *et al*., 2021). In the same vein, genome-wide association studies (GWAS) have been used to identify genomic regions controlling plant architecture and yield-related traits in several crop plants, including hexaploid wheat (Muhammad *et al*., 2021), rice (Chen *et al*., 2014), and landraces of soybean (Zhang *et al*., 2021). Through these studies, significant SNPs and candidate genes that influence growth and development were identified.

These findings present huge potential for crop improvement through marker-assisted selection and genomic selection.

The objective of this study was to investigate the genetics of plant architecture and yield traits in cassava using a genome-wide association study.

3.2 Materials and Methods

The cassava accessions used for this research were developed by the cassava breeding unit of the International Institute of Tropical Agriculture (IITA), Ibadan. The accessions used were obtained from the clonal evaluation trial of the breeding program. Four hundred and forty-eight accessions from the clonal evaluation trial were advanced to the preliminary yield trial stage. The collection of genotypes used for this trial comprised 453 cassava accessions, including 448 accessions that were selected from the clonal evaluation trial and five commercial varieties used as checks in the experiment. The details of the accessions, including those of the crosses/parents used, are contained in Table 3.1 of the supplementary file. The description of the commercial check varieties is shown in Table 3.1 of the appendices. The trial was conducted in three locations (Table 3.1) across two planting seasons (2020/2021 and 2021/2022) in Nigeria. The trial was laid out in a modified augmented block design with two replications per environment (location x season). Genotypes were assigned to incomplete blocks nested within replicates to control for field heterogeneity. The field layout contained both row and column coordinates, which allowed spatial modelling to account for possible field trends. Two to three commercial check varieties were included in each block to provide benchmarks for performance comparison and quality control. A plot comprises three rows with three plants planted on ridges per row. A spacing of 1.0 m was maintained between ridges, while a spacing of 0.8 m was observed within plants in a row.

Table 3.1The coordinates and weather data for the trial locations in Nigeria

Location	GIS Coordinates	Altitude (MASL)	Average Rainfall (mm)	Average Temperature (°C)	Agroecological Zone
Ikenne	Lat 6.8718° N, Long 3.7106° E	90	2,000	27	Humid Forest
Onne	Lat 4.7363° N, Long 7.1545° E	6.8	2,700	26	Humid Forest
Mokwa	Lat 9.2934° N, Long 5.0493° E	180	1,200	32	Southern Guinea Savannah

MASL – Meters Above Sea Level, mm – Milimeters, °C – Degrees Celcius

3.2.1 Phenotypic Data Collection

At specific phenological stages of the crop (3, 6, 9 and 12 months after planting), measurements were taken for the plant architecture and yield-related traits: The phenological stage and method used in measuring the traits in cassava were based on the guidelines outlined in Fukuda *et al*. (1998) and the NEXTGEN cassava trait ontology standard evaluation procedure contained in the (CassavaBase). The details of the trait evaluation are herein stated:

Plant height was measured from the soil surface to the tip of the main stem at 3, 6, 9 and 12 months after planting (MAP). Height at the first branch was measured from the soil surface to the base of the first branch at 3, 6, 9 and 12 MAP. The angle of branching was measured as the angle between the main stem and the first branch at 9 MAP. Level of branching was measured as the number of branches per plant at 3, 6, 9 and 12 MAP. Branching habit was measured as the orientation of the branches (Erect, Dichotomous, Trichotomous and Tetrachotomous) at 9 MAP. Stem diameter was measured as the thickness of the main stem at 20 cm above the soil surface at 9 MAP. Dry matter content was measured at harvest (12 MAP) using the specific gravity method as described in Fukuda et al. (1998). The number of lodged plants per plot was counted and recorded; this entails plants that fell over or lodged at the base due to wind or pests at 9 MAP. Fresh root weight was measured as the total weight of fresh roots harvested per plot at harvest. Shoot weight was measured as the total weight of aboveground biomass (stems and leaves) per plot at harvest (12 MAP). Fresh root yield was calculated at harvest (12 MAP) by dividing the fresh root weight per plot by the highest number of stands harvested per plot and multiplied by 12,000 divided by 1000 which gives the value of the fresh root yield in tons per hectare. Top yield was calculated at harvest (12 MAP) by dividing the shoot weight per plot by the highest number of stands harvested per plot and multiplied by 12,000 divided by 1000 which gives the value of the top yield in tons per hectare. Dry yield was calculated at harvest (12 MAP) by dividing the value of fresh root yield by the value of the dry matter content multiplied by 100. The following traits: fresh root yield, dry yield, and top yield, were estimated in line with the protocol described by Hauser (2023) in the standard operating procedure for yield estimation in cassava. Harvest index was measured at harvest (12 MAP) as the ratio of fresh root weight to shoot weight per plot at harvest. Number of plants per stand was calculated at (9 MAP) as the number of plants that stemmed from each plant stand.

3.2.2 SNP Genotyping and SNP Filtering

At one month after planting, fresh young leaves were collected from each cassava accession. The fresh leaves were freeze-dried in a vacuum following the Diversity Arrays Technology Pty Ltd protocol (*Diversity Arrays Technology | Genotyping & Data Analysis Experts*). The freeze-dried leaf samples were shipped to Diversity Arrays Technology Pty Ltd (*Diversity Arrays Technology | Genotyping & Data Analysis Experts*) for genotyping using the DArTseq platform. This platform uses genome complexity reduction-based sequencing technology to systematically select the regions of a genome that are mostly active and have low copy sequence (Cruz *et al*., 2013). SNP calling was performed using the TASSEL 5.2.90 pipeline (Bradbury *et al*., 2007). A panel of 61,238 SNP markers were recovered from the raw dataset. The PLINK 1.9 software (Chang *et al*., 2015; Purcell *et al*., 2007) was deployed to filter the SNP markers.

3.2.3 Marker Filtering and Statistical Analyses of Phenotypic Data

SNP markers with less than 5% minor allele frequency (MAF) and more than 10% missing call rate were pruned out of the genotypic data. Likewise, nineteen accessions with missing data for more than 10% of the SNP markers were excluded from the marker-trait analysis. Four hundred and thirty-four accessions and 54,574 SNP markers distributed across the eighteen chromosomes in the cassava genome were used in the genome-wide association (GWAS) analysis.

The plant architecture and yield traits were analyzed with the spatial single trial model fitted using the `SpATS` package v1.0-9 (Rodríguez-Álvarez *et al*., 2018) of the R software (R Core Team, 2020). The mathematical formula of the adopted model is herein stated:

$$y_{ijk} = \mu + g_i + r_j + b_k + s(x_{ijk}, y_{ijk)} + e_{ijk}$$

Where y_{ijk} - the phenotypic value of the i^{th} genotype in the j^{th} block and the k^{th} incomplete block; μ is the overall mean; g_i is the random effect of the i^{th} genotype; r_j is the random effect of the j^{th} block; b_k is the random effect of the k^{th} incomplete block; $s(x_{ijk}, y_{ijk})$ is the smooth bivariate function of the row and column coordinates of the plot and e_{ijk} is the residual error.

The best linear unbiased prediction (BLUP) values derived from this model were used as phenotypic values in the marker-trait association analysis. Broad sense heritability values were estimated in the SpAT package through the formula described by Schmidt *et al*. (2019) as follows:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_s^2 + \sigma_e^2}$$

Where H^2 is the broad sense heritability estimate, $\sigma^2 g$ is the variance component of the genotype effect, $\sigma^2 s$ is the variance component of the spatial P-spline component, $\sigma^2 e$ is the variance component of the residuals.

The estimation of genetic advance as a percentage of mean (GAM) was performed using the formula described in (Johnson *et al*., 1955).

$$GAM = \frac{K \times \sigma p \times H}{X} \; X\,100$$

Where:

K = 2.06 at 5% selection intensity.

H = Heritability.

σp = Phenotypic standard deviation.

X = Mean.

Johnson *et al*. (1955) grouped GAM into 3 categories as follows:

GAM values that were less than 10% were low, values between 10-20% were classified as moderate while values that were more than 20% were high.

For the multi-environmental trial analysis, the linear mixed model was fitted as follows, using the lmer function from the lme4 package (Bates *et al*., 2015) of the R software (R Core Team, 2020).

$$\eta_{ijklm} = \mu + \alpha_i + \beta_{ij} + \gamma_k + \delta_{ik} + \epsilon_{ijl} + e_{ijkl}$$

Where η_{ijklm} is the yield value for the m^{th} plot in the l^{th} block of the j^{th} replicate of the i^{th} environment for the k^{th} accession; μ is the overall mean; α_i is the fixed effect of the i^{th} environment; β_{ij} is the fixed effect of the interaction between the i^{th} environment and the j^{th} replicate; γ_k is the random effect of the k^{th} accession; δ_{ik} is the random effect of the interaction between the i^{th} environment and the k^{th} accession; ϵ_{ijl} is the random effect of the interaction between the i^{th} environment, the j^{th} replicate, and the l^{th} block; and e_{ijkl} is the random residual error.

The random effects γ_k, δ_{ik}, and ϵ_{ijl} are assumed to be independent and normally distributed with mean of zero and variance components σ^2a, σ^2ea, and σ^2b, respectively. The residual error e_{ijkl} is also assumed to be independent and normally distributed with mean of zero and variance component σ^2e.

The best linear unbiased prediction (BLUP) values derived from this model were used as pooled phenotypic values across environments. The broad sense heritability (H^2) values were calculated as follows:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e^2}{er}}$$

Where H^2 is the broad sense heritability estimate, σ^2g is the genetic variance component of the accession effect, σ^2ge is the variance component of the genotype by environment effect, σ^2e is the variance component of the residual error, e is the number of environments and r is the number of replicates.

3.2.3.1 Marker Coverage and SNP Density

The marker coverage and SNP density analysis and visualisation were performed using the SRplot platform for data visualization and graphing (Tang *et al*., 2023).

3.2.3.2 Linkage Disequilibrium Analysis

Pairs of markers with perfect LD scores of (r^2 =1) were removed prior to further analysis. The LD analysis and LD decay plot were performed using both TASSEL 5.2.90 and PLINK 1.9 software (Chang *et al*., 2015; Purcell *et al*., 2007) and visualization of the output in the R software (R Core Team, 2020).

3.2.3.3 Population Structure Analysis

Population structure analysis was performed using ADMIXTURE (Alexander *et al*., 2009) which used the maximum likelihood estimate to assign genotypes to putative populations (K). Cross-validation was used to determine the optimal number of clusters. The outcome of the population structure analysis was visualized using the "ggplot2" package (Wickham, 2016). Hierarchical clustering was performed using the Ward's minimum variance method (ward.D2) on the Q-matrix generated by ADMIXTURE. The R package "dendextend" (Galili, 2015) was used to plot the dendrogram.

3.2.3.4 Genetic Association Analysis

The marker-trait association analysis for each trait was performed with a Mixed linear model (MLM) (Zhang *et al*., 2010). Due to the inability of this model to detect significant peaks of SNPs, another model; Fixed and random model Circulating Probability Unification (FarmCPU) (X. Liu *et al*., 2016) was tested using the GAPIT (Genome Association and Prediction Integrated Tools) R package (Lipka *et al*., 2012).

3.2.3.5 Mathematical formulae of the GWAS model:

MLM: Mixed Linear Model. This model decomposes the observed phenotype (y) into fixed effects (Xβ), random genetic effects (Zu), and residual effects (e). The formula is:

$y = X\beta + Zu + e$

where X is the design matrix for fixed effects, Z is the design matrix for random effects, β is the vector of fixed effects, u is the vector of random effects, and e is the vector of residuals.

FarmCPU: Fixed and random model Circulating Probability Unification. This model uses a modified MLM method, Multiple Loci Mixed Model (MLMM), and incorporates multiple markers simultaneously as covariates in a stepwise MLM to partially remove the confounding between testing markers and kinship. The formula is:

$$y = X\beta + Z_1u_1 + Z_2u_2 + e$$

where X is the design matrix for fixed effects, Z_1 is the design matrix for random effects from kinship, Z_2 is the design matrix for random effects from multiple markers, β is the vector of fixed effects, u_1 is the vector of random effects from kinship, u_2 is the vector of random effects from multiple markers, and e is the vector of residuals.

These models deployed different approaches in precluding any possibility of false discovery.

3.2.3.6 Criteria for declaration of significant SNP markers

The following criteria were used in calling SNPs that share a significant correlation with the plant architecture and yield traits: Bonferroni correction, the threshold of the P-value, Manhattan plot and the QQ plot.

The SNPs with significant associations with the plant architecture and yield traits were called based on the p-value thresholds and visualizations (Manhattan and QQ plots).

Based on the Bonferroni correction for multiple testing on SNPs, the genome-wide significance threshold was set at α = - log10(0.05 / number of SNPs) = (2 x 10^-6) for potentially significant candidate SNPs.

The Manhattan plot visualized the distribution of -log10(p-values) for all SNPs across the genome. A clear inflation and upward deviation of data points relative to the expected line indicates potential non-random association patterns.

The QQ plot compared the observed distribution of p-values against the expected uniform distribution under the null hypothesis (no association). A strong deviation of observed p-values from the expected line, particularly in the tail, would suggest inflated test statistics and potential false positives. These informed the decision to declare the selected SNPs in this analysis as SNPs with significant associations with plant architecture and yield traits.

3.2.3.7 Candidate Gene Analysis

Significant SNPs obtained from the marker-trait association analysis were used in predicting the candidate genes. The highlighted SNP markers were mapped onto genes within the 5,000 bp windows using the Manihot esculenta v7.1 of the Phytozome genome browser (Goodstein *et al*., 2014; Goodstein *et al*., 2012). The uniprott consortium database, Aleksander *et al*. (2023), was used in performing the gene ontology annotation.

3.3 Results

3.3.1 Marker Coverage and SNP Density

All the 434 accessions with 54,574 SNP markers distributed across the eighteen chromosomes in the cassava genome obtained from the genotypic data filtering were used in the genome-wide association (GWAS) analysis. The SNPs were not evenly distributed across the 18 chromosomes (Figure 3.1). Chromosome 1 had the highest number of SNPs (7235) with an average of 207 SNPs/Mb, while chromosome 7 had the fewest SNPs (1588) with approximately 59 SNPs/Mb.

3.3.2 Linkage Disequilibrium:

The linkage disequilibrium (LD) decay plot (Figure 3.2) shows the relationship between the distance between pairs of genetic markers (base pairs) and the squared correlation coefficient (r^2) of allele frequencies at those pairs of markers.

The LD decay plot shows that LD decays rapidly with distance. In this case, the LD between two SNPs falls to 0.2 (the standard threshold that indicates the end of LD) at approximately 125,000 bp. This suggests that the genes in this population are well-mixed, and there has been little recent recombination between them.

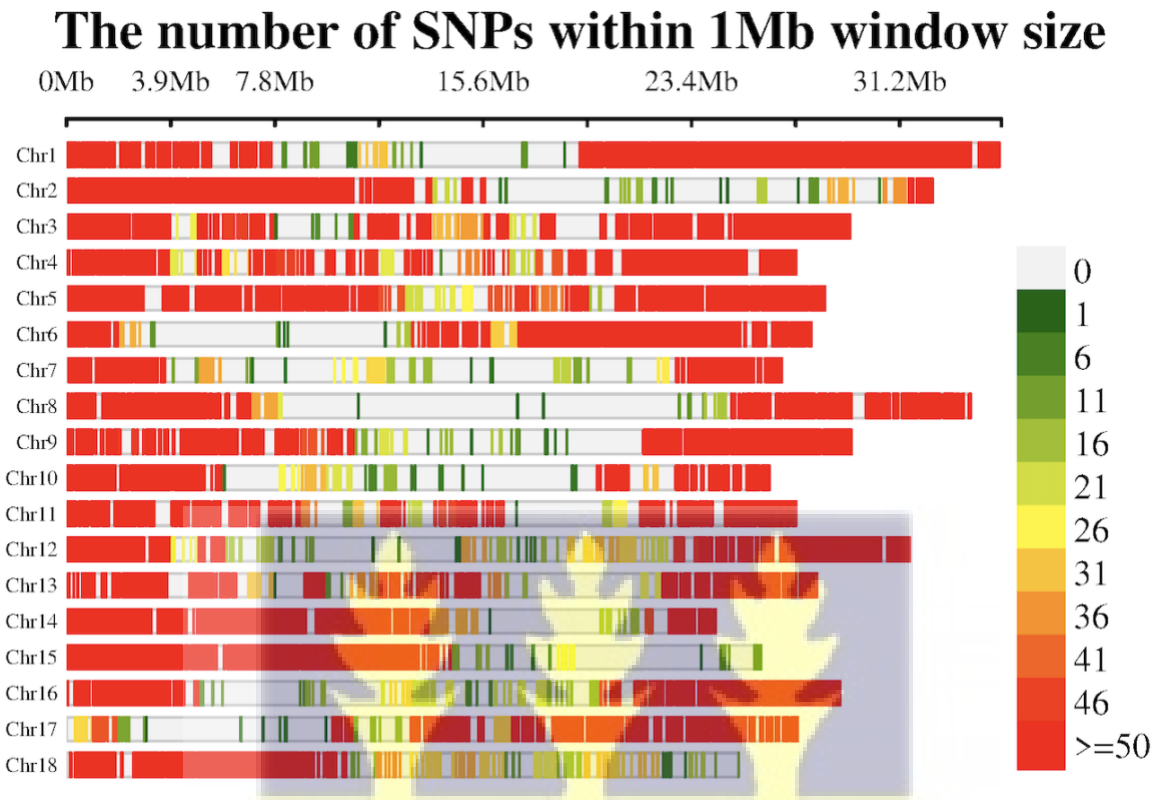

Figure 3.1| The SNP density plot that shows the distribution of SNPs across the chromosomes within 1Mb window size of the *Manihot esculenta* genome.

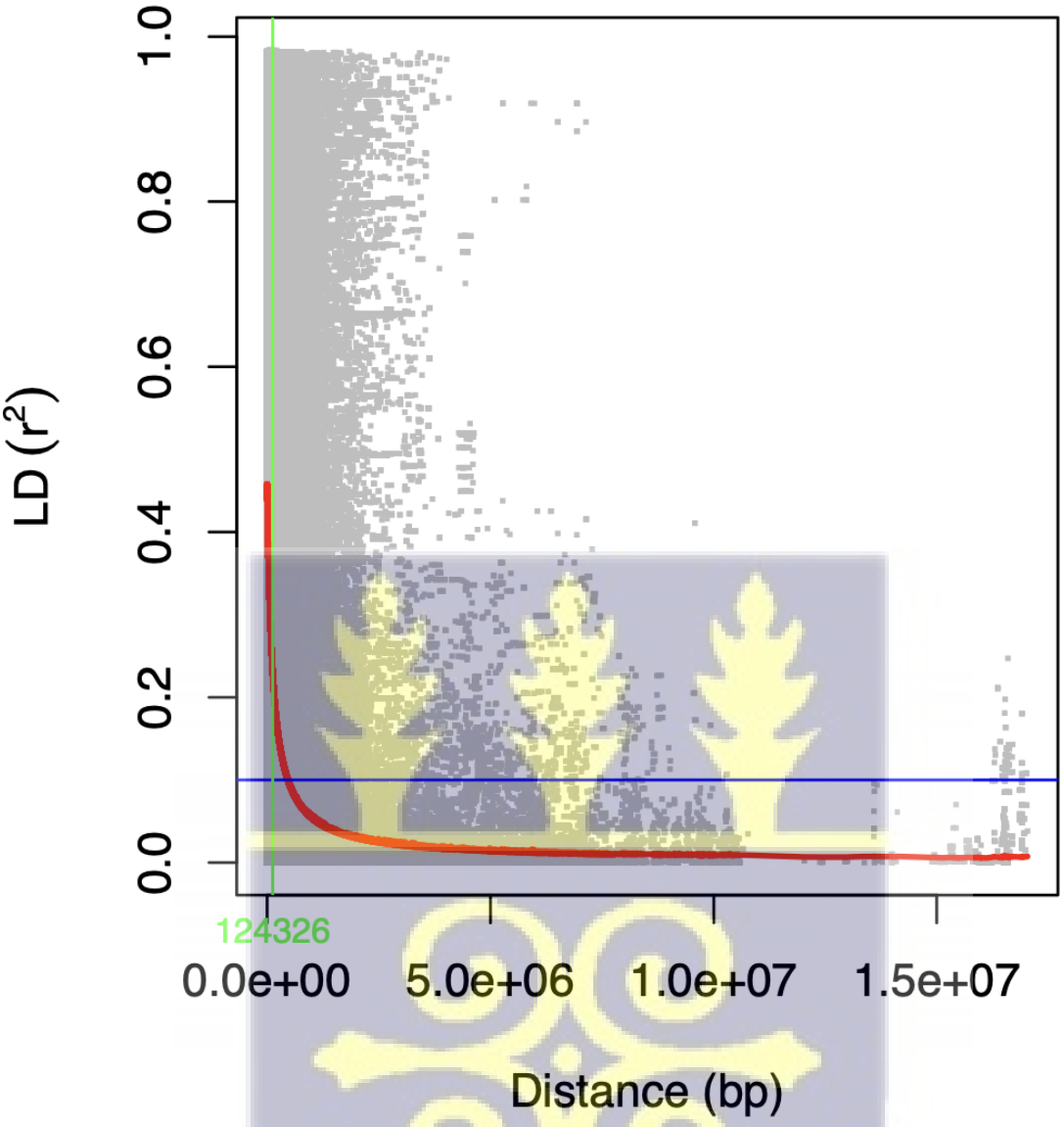

Figure 3.2|The LD decay plot performed with TASSEL and visualized in R.

3.3.3 Population Structure Analysis

Population structure is one of the underlying factors that determines the effectiveness of a genome-wide association study and its ability to accurately identify candidate genes that are associated with the traits under review (Yu *et al.*, 2006). Admixture software that uses the Bayesian-based clustering analysis was used in determining the population structure of the 434 cassava accessions used in this trial. The admixture plot of the population structure analysis (Figure 3.3) revealed that there are five subgroups in this population. The plot also shows that there is a balance between the extent of admixture and homogeneity within the population. This shows that there exists enough genetic diversity within the population to capture the variation in the plant architecture and yield traits.

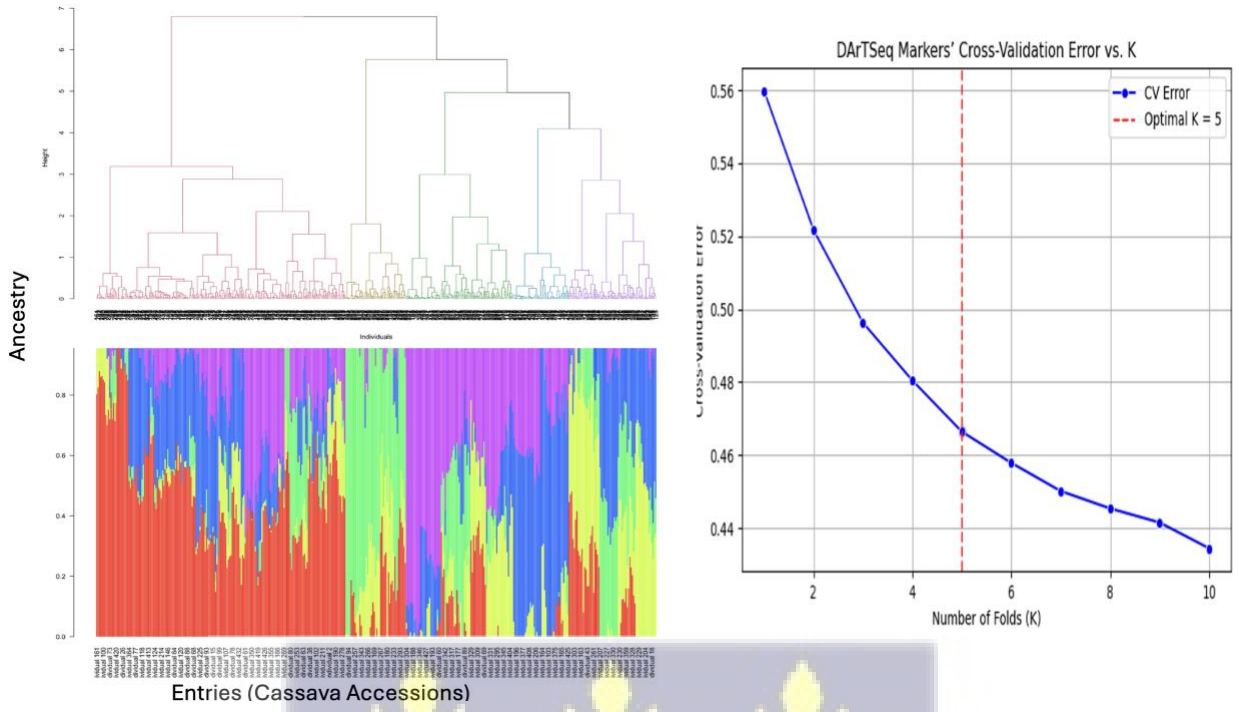

Figure 3.3| Admixture plot showing clustering of 434 cassava accessions into clusters based on the molecular data using Bayesian-based clustering analysis.

3.3.4 Variance Components, Broad Sense Heritability and Genetic Advance of Plant Architecture and Yield Traits

The genotypic variance was higher than the error variance for all the 18 traits (Table 3.2). The pooled values of the broad sense heritability for the 18 traits studied in this trial ranged from moderately high (0.62) for shoot weight and top yield to moderately high (0.88) for height at the first branch at 9 months after planting and harvest index. High broad sense heritability values were observed for height at the first branch at 6 months after planting (0.86), 9 months after planting (0.88), plant height at 6 months after planting (0.83), 9 months after planting (0.8) and harvest index (0.86). Similarly, the moderately high values of broad sense heritability were reported for the following yield determining traits: dry matter content (0.68), starch content (0.7) and fresh root yield (0.67) (Table 3.2). The phenotypic and genotypic coefficient of variation ranged from 8.29% and 6.84% respectively for dry matter content to 32.4% for fresh root yield and 29.53% for height at the first branch at 6 months after planting respectively (Table 3.2). The lowest value of genetic advance (0.19) was observed on harvest index while the highest value of 46.56 was recorded on height at the first branch at 9 months after planting. The lowest value for genetic advance as a percentage of the mean 11.65 was realized from dry matter content while the highest value of 56.39 was recorded on the height at the first branch at 6 months after planting (Table 3.2).

Table 3.2 | Estimates of variance components, broad sense heritability, PCV, GCV, and genetic advance for plant architecture and yield traits in 453 cassava accessions evaluated across three locations in Nigeria.

Trait	Mean	σ^2_g	σ^2_{GxE}	σ^2_e	H^2	PCV(%)	GCV(%)	GA	GAM
STMDI9	24	5.56	0.81	1.28	0.73	11.52	9.82	4.15	17.3
FYLD	23	37.2	9	9.32	0.67	32.4	26.52	10.31	44.83
DYLD	7.8	3.7	0.97	1.08	0.64	30.74	24.66	3.19	40.85
STARCH	19.8	5.84	1.71	0.85	0.7	14.63	12.21	4.16	21.02
DM	32.6	4.97	1.53	0.8	0.68	8.29	6.84	3.8	11.65
RTWT	19.2	25.5	6.67	6.43	0.66	32.36	26.3	8.48	44.14
SHTWT	21	21.8	4.73	8.5	0.62	28.19	22.23	7.61	36.22
PLTHT9	176.9	507.8	40.83	84.67	0.8	14.23	12.74	41.67	23.55
HI	0.47	0.01	0	0	0.86	22.98	21.28	0.19	40.68
BRNHB9	2.6	0.17	0.04	0.03	0.71	18.78	15.86	0.72	27.66
ANGBR9	81	60.7	6	10.93	0.78	10.88	9.62	14.23	17.56
RTNO	44.6	131.4	29.87	41.58	0.65	31.93	25.7	19.05	42.72
PPSTD9	2	0.1	0.01	0.05	0.63	19.9	15.81	0.52	25.95
BRNHT9	83.8	580	33.63	48	0.88	30.69	28.74	46.56	55.56
PLTHT6	158	459	30.57	64.67	0.83	14.9	13.56	40.26	25.48
TYLD	25.9	31.5	6.4	13.17	0.62	27.59	21.67	9.1	35.14
BRNHT6	74	477.6	36	44.93	0.86	31.94	29.53	41.73	56.39
BRLEV9	2.3	0.34	0.06	0.03	0.78	28.62	25.35	1.07	46.37

STMDI - stem diameter, FYLD - fresh root yield, DYLD - dry yield, STARCH – starch content, DM – dry matter content, RTWT – fresh root weight, SHTWT – shoot weight, PLTHT9 – plant height at 9 months after planting, LODG – number of lodged plants per plot, HI – harvest index, BRNHB9 – branching habit at 9 months after planting, ANGBR9 – angle of branching, RTNO – number of harvested roots, PPSTD9 – number of plants per stand, BRNHT9 – height at the first branch at 9 months after planting, PLTHT6 – plant height at 6 months after planting, TYLD – top yield, BRNHT6 – height at the first branch at 6 months after planting. $\sigma^2 g$ – genotypic variance, $\sigma^2 e$ – residual variance, $\sigma^2 p$ – phenotypic variance, H^2 - broad sense heritability, PCV, phenotypic coefficient of variation, GCV- genotypic coefficient of variation, GA - Genetic advance, GAM - genetic advance as a percentage of mean.

3.3.5 Results of Marker-Trait Analysis

All the 18 traits studied were subjected to GWAS analysis. Only eight traits had significant SNPs (Table 3.3), this was confirmed based on the position of the SNPs above the cut-off points in the Manhattan plot and consistency of the QQ plots (Figure 3.1) of the appendices. These eight traits are: angle of branching, plant type, overall plant appearance, level of branching at 6 months after planting, dry matter content, level of branching at 9 months after planting, harvest index and number of harvested plants per plot. All the 17 significant SNPs recorded for these traits were found on chromosomes 1, 3, 4, 5, 6, 8, 9, 11, 12, 15 and 16. The SNPs reported in this study were obtained from the GWAS analysis conducted with the Fixed and random model Circulating Probability Unification (FarmCPU) model (Liu *et al*., 2016).With the aid of the *Manihot esculenta* v7.1 of the Phytozome genome browser (Goodstein *et al*., 2014; Goodstein *et al*., 2012), the genomic regions within the 5,000 kb window of the significant SNPs were further investigated to find annotated genes and establish their potential functions. The candidate genes that were near the significant SNPs have been identified and were shown in (Table 3.4).

Table 3.3 | Statistical summary of top significant SNPs at each major trait-linked locus for plant architecture and yield traits of cassava.

Trait	SNP_ID	Chromosome Number	Position	Value of P	Minor Allele Frequency	Phenotypic Variance Explained
Angle of Branching	S1_19494690	1	19494690	$6.77E^{-07}$	0.15944	0.85688
	S1_23883230	1	23883230	$4.58E^{-07}$	0.19515	18.5628
Plant Type	S3_1388806	3	1388806	$1.17E^{-07}$	0.46495	0
	S5_10702830	5	10702830	$1.80E^{-08}$	0.44393	3.88491
	S15_10073295	15	10073295	$2.78E^{-07}$	0.1729	1.60299
Overall Plant Appearance	S4_5944464	4	5944464	$2.94E^{-08}$	0.42523	1.12237
	S16_2295914	16	2295914	$2.73E^{-08}$	0.30958	1.87443
	S17_17302312	17	17302312	$5.68E^{-08}$	0.43107	5.10115
Level of Branching at 6 months after planting	S8_27519983	8	27519983	$5.53E^{-07}$	0.15278	18.6092
	S11_16097795	11	16097795	$5.67E^{-08}$	0.10301	15.8714
Level of Branching at 9 months after planting	S5_22148410	5	22148410	$1.20E^{-09}$	0.45718	0.61819
	S11_16097795	11	16097795	$3.30E^{-08}$	0.10301	22.6755
Dry Matter Content	S16_24715889	16	24715889	$1.33E^{-08}$	0.14419	24.3844
Harvest Index	S9_3493565	9	3493565	$1.32E^{-13}$	0.31481	5.37937
	S12_29499402	12	29499402	$1.81E^{-07}$	0.4456	5.60214
	S16_22907596	16	22907596	$1.43E^{-08}$	0.06134	7.05957
Number of harvested Plants	S6_21336567	6	21336567	$9.00E^{-07}$	0.08912	32.7769

Table 3.4 | Gene annotation for the significant SNPs for plant architecture and yield traits.

Trait	Marker	Position	Chromosome	Gene ID	Gene Annotation
Angle of Branching	S1_19494690	19494690	1	Manes.01G056000	glucan endo-1,3-beta-D-glucosidase
				Manes.01G056100	Ubiquitin carboxyl-terminal hydrolase
	S1_23883230	23883230	1	Manes.01G077800	Nitrate-transporting ATPase
				Manes.01G077900	Uncharacterized Manes.01G077900
Plant Type	S3_1388806	1388806	3	Manes.03G016100	DYW domain-containing protein
				Manes.03G016200	AAA+ ATPase domain-containing protein
				Manes.03G016300	Adenine Nucleotide Transporter
	S15_10073295	10073295	15	Manes.15G122400	9-cis-epoxycarotenoid dioxygenase
Overall Plant Appearance	S4_5944464	5944464	4	Manes.04G041500	RBR-type E3 ubiquitin transferase
	S16_2295914	2295914	16	Manes.16G020700	F-box domain-containing protein
Level of Branching at 6 Months after Planting	S11_16097795	16097795	11	Manes.11G089900	Triosephosphate isomerase
Level of Branching at 9 Months after Planting	S5_22148410	22148410	5	Manes.05G148900	Cytokinin riboside 5'-monophosphate phosphoribohydrolase
				Manes.05G148800	Endoglucanase
				Manes.05G148700	Myb/SANT-like domain-containing protein
	S11_16097795	16097795	11	Manes.11G089900	Triosephosphate isomerase
Dry Matter Content	S16_24715889	24715889	16	NA	NA
Harvest Index	S9_3493565	3493565	9	Manes.09G018900	Glycosyltransferase
	S12_29499402	29499402	12	Manes.12G109600	RING-type E3 ubiquitin transferase
	S16_22907596	22907596	16	Manes.16G062600	JmjC domain-containing protein
Number of harvested Plants	S6_21336567	21336567	6	Manes.06G073700	TauD/TfdA-like domain-containing protein

3.4 Discussion:

Broad sense heritability is a measure of the proportion of the total phenotypic variation in a trait that is due to genetic factors. It is an essential parameter in plant breeding, as it indicates the potential for genetic improvement of a trait through selection. In this study, a couple of plant architecture and yield-related traits have been reported to have moderately high to high broad sense heritability, including Fresh Root Yield (0.67), Dry Matter Content (0.8), Harvest Index (0.86), height at the first branch at 6 months after planting (0.86), height at the first branch at 9 months after planting (0.88), Plant height at 9 months after planting (0.8), and Starch Content (0.7). Similar results were reported by Santos *et al*. (2023) on fresh root yield and dry matter content. High starch content is one of the selling points of cassava varieties targeted for industrial use. The high value of broad sense heritability recorded for starch content in this study was corroborated by the findings of Oliveira *et al*. (2015).

Following the classification of Johnson *et al*. (1955) who categorized estimates of genetic advance as a percentage of mean (GAM) that were less than (10%) as low, those that ranged between (10-20%) as moderate and those more than (20%) as high, the observed GAM values in this experiment ranged from moderate to high and it confirms that these traits were not only highly heritable but will also respond favourably to selection. The combination of moderately high to high estimates of broad-sense heritability and GAM for key traits indicates a strong potential for their genetic improvement through phenotypic selection.

For example, selection for Fresh Root Yield, which has a heritability of 0.67 and GAM value of 45% implies that imposing selection pressure on the top 5% of the base population could result in significant gains of 45% in yield over time. Similarly, selection for Dry Matter Content and Starch Content, both of which have heritability estimates of 0.8 and 0.85, and GAM values of 11% and 21% respectively could result in increase of 11% and 21% respectively, thereby improving the quality of cassava roots for industrial processing and consumption. In addition to the potential for genetic improvement through selection, these moderate to high heritability estimates suggest that these traits are relatively stable across environments and are not significantly influenced by environmental factors. This means that selection for these traits is likely to be effective despite environmental variability.

3.4.1 Candidate Genes for Angle of Branching:

Angle of branching profoundly influences light interception and canopy architecture (Tang et al., 2019). In the current study two significant SNPs and four candidate genes associated with the branching angle were identified.

Among the candidate genes, Manes.01G077900 found in the domain of the significant SNP S1_23883230 on chromosome 1 is a novel gene. The three remaining candidate genes were found to encode for enzymes that are likely to be involved in the regulation of angle of branching in cassava. One of these genes Manes.01G077800 is in proximity with the significant SNP S1_23883230 found on chromosome 1. This gene encodes Nitrate-transporting ATPase (NtATPase). The *Nitrate Transporter 1 (NRT1*) of the *Nitrate Transporter 1/Peptide Transporter Family* (*NPF*) gene family is responsible for coding the Nitrate-transporting ATPase (NtATPase) protein complex that mediates the active transport of nitrate across the plasma membrane of plant cells. Functions of the NtATPase include nitrate uptake, sensing, and signalling in plants, and it can affect the growth, development, and stress responses of crop plants (Fan *et al*., 2017). According to Zhang *et al*. (2018), NtATPase could regulate shoot growth and root architecture by modulating nitrate distribution and signalling between different plant tissues and organs. Ibrahim *et al*. (2017) reported that introducing the maize *nitrate transporter* gene *ZmNrt2.1* into tobacco altered its growth response and improved root and shoot growth and development.

The second candidate gene is Manes.01G056100. It is co-localized with the significant SNP S1_19494690, which is also located on chromosome 1. The function of this gene involves the encoding of ubiquitin carboxyl-terminal hydrolases (Aleksander *et al*., 2023). Yang *et al*. (2007) reported the roles of two related *ubiquitin carboxyl-terminal hydrolases* (*UCHs*) genes, *UCH1* and *UCH2*, in Arabidopsis. The authors stated that these genes regulate ubiquitin levels and affect shoot architecture by modulating auxin and cytokinin signalling pathways. They also stated that the overexpression of either *UCH1* or *UCH2* enhances the outgrowth of cauline lateral branches, confirming the role of these genes in branching events in crop plants. Also, the third candidate gene Manes.01G056000, which is found in the domain of SNP S1_19494690 on chromosome 1 encodes glucan endo-1,3-beta-D-glucosidase (Aleksander *et al*., 2023). This glucan endo-1,3-beta-D-glucosidase is an enzyme with diverse functions and it plays critical roles in plant defence, development and response to stress (Johnson *et al*., 1955).

3.4.2 Candidate Genes for Plant Type

Growth habit and overall morphology of the cassava plant characterize plant type. It can be classified into four main types: compact, open, umbrella and cylindrical. Various factors, such as stem length, internode length, and branching pattern, determine plant type.

It has significant impacts on planting density and resource utilization. The genes of interest are crucial to development, response to stress, adaptation, and evolution in plants, which likely contribute to the determination of cassava plant type. The highlighted candidate genes are:

Manes.03G016100, which was identified near the significant SNP S3_1388806 found on chromosome 3. This gene is responsible for the coding of *DYW* domain-containing protein. The abbreviation "*DYW*" in the context of *DYW* domain-containing protein stands for a conserved motif sequence of three amino acids: Aspartate (D), Tyrosine (Y), and Tryptophan (W). *DYW* domain-containing protein gene is a pentatricopeptide repeat (PPR) gene involved in RNA editing in plant organelles. RNA editing is a process that alters the nucleotide sequence of RNA transcripts, affecting their function and expression. Flint-Garcia (2013) found that domesticated crops have more RNA editing sites than their wild relatives, suggesting that RNA editing is essential for plant adaptation and evolution. The author also identified several candidate genes differentially edited between domesticated and wild plants, such as flowering time, starch metabolism, and stress response. These genes may have contributed to the phenotypic changes during crop domestication. According to Li *et al*. (2021), PPR proteins are induced by abiotic or biotic stresses and modulate the expression of genes related to stress tolerance or defence response in plant mitochondria or chloroplasts.

The candidate gene, Manes.03G016200, was also near the SNP S3_1388806 on chromosome 3. This gene encodes AAA+ ATPase domain-containing proteins (Aleksander *et al*., 2023).

The functional expressions of genes that code for AAA+ ATPase domain-containing proteins have varying effects on crop plants depending on the specific protein and its function. Xu *et al*. (2018) have linked the product of CsARN6.1, a gene that encodes an AAA ATPase domain-containing protein with tolerance to waterlogging stress in cucumber plants. It promotes adventitious root formation and increases the number of adventitious roots (ARs) through ATPase activity. Transgenic cucumber plants that expressed CsARN6.1 showed better rooting ability and lateral root development. Similarly, Xia *et al*. (2013) highlighted the role of the product of the maize gene (*ZmSKD1*) that encodes AAA+ ATPase domain-containing proteins in improving the ability of transgenic tobacco plants to withstand salt and drought stress. The overexpression of ZmSKD1 resulted in increased salt and drought stress tolerance, suggesting its involvement in stress responses in crop plants. According to Zhu *et al*., (2016), in addition to these functions the LRD6-6 protein, an AAA ATPase domain-containing protein localized in multivesicular bodies (MVBs) in rice, has been found to inhibit immunity and cell death in rice plants. It likely regulates MVBs-mediated vesicular trafficking, which plays a role in plant immunity (Zhu *et al*., 2016).

Another gene that was identified within the range of the SNP S3_1388806 on chromosome 3 is Manes.03G016300. The functional product of this gene is Adenine nucleotide transporter BT1 (Aleksander *et al*., 2023). According to Witte & Herde (2020), *Adenine nucleotide transporter BT1* (*Brittle1*) is a protein that is enclosed in the inner envelope membrane of plastids, such as chloroplasts, and is a member of the *mitochondrial carrier family* (*MCF*). It affects various aspects of plant development and stress responses, such as seed germination, photosynthesis, starch metabolism, circadian rhythm, senescence and resistance to pathogenic infections (Witte & Herde, 2020). According to Soliman *et al*. (2014), *BT1* may affect the starch biosynthesis in crop plants by transporting ADP-glucose, the primary precursor for starch synthesis, into the amyloplasts of endosperm cells. The authors reported that mutation in BT1 reduced barley's starch content and brittle grains. This could provide an enhanced insight into the genetic basis of starch biosynthesis in cassava to improve starch content in cassava for industrial use. Another SNP, S15_10073295, correlated to plant type was found on chromosome 15. This SNP is co-localized with the gene Manes.15G122400, which encodes for an enzyme known as 9-cis-epoxycarotenoid dioxygenase (Aleksander *et al*., 2023). 9-cis-epoxy carotenoid dioxygenase (NCED) is a critical enzyme in the biosynthesis of abscisic acid (ABA). This plant hormone is essential for the growth, development, and defence against abiotic stress of plants (Gupta *et al*., 2022; Zhang *et al*., 2009). According to reports by the following authors, the effects of NCED on plant growth could either be positive or negative: He *et al*. (2018) observed that overexpression of NCED in grapevine resulted in faster growth rate, longer shoot length, and better drought resistance, also in rice, the overexpression of NCED enhanced plant growth and multi-abiotic stress tolerance (Huang *et al*., 2018). However, in sweet potatoes, overexpression of NCED negatively regulated plant height, where transgenic plants showed a dwarf phenotype with lower plant height than the wild type (Zhou *et al*., 2023).

3.4.3 Candidate Genes for Overall Plant Appearance

Overall Plant Appearance provides a holistic assessment of plant health, vigor, and overall phenotypic acceptability. Various factors influence overall plant appearance, such as genotype, environment, stress, and disease. The candidate genes that were identified for this trait were implicated in plant development, architecture, and productivity. This underscores their potential roles in influencing cassava's visual appearance and growth under varying conditions.

The most significant SNP for overall plant appearance SNP, S4_5944464, was located on chromosome 4, near the candidate gene Manes.04G041500, which encodes for RBR-type E3

ubiquitin transferases (Aleksander *et al*., 2023). The *Ring-Between-Ring* (*RBR*) *type E3 ubiquitin transferases* have been found to regulate abscisic acid (ABA) receptor levels and signalling (Singh *et al*., 2022). A review of the soybean ubiquitin-proteasome system, which includes RBR-type E3 ubiquitin ligases, shows that overexpression of *Glycine max WRINKLED1b* (*GmWRI1b*) has a significant influence on plant architecture through increased node number, stem diameter, pod number per plant, and yield per plant (Xiong *et al*., 2023).

On chromosome 16, another SNP, S16_2295914, shared an association with overall plant appearance, and the corresponding gene in the vicinity of this SNP is Manes.16G020700. This gene is involved in the coding of F-box domain-containing protein (Aleksander *et al*., 2023). F-box proteins have been found to play a role in various aspects of plant development, including root development, leaf and stem development, and flower and fruit development. This suggests that the F-box domain-containing protein is involved in shaping the overall architecture of the plant (Xu *et al*., 2021). This is in agreement with the findings of Hong *et al*. (2020), who reported the expression profiles of F-box genes at different developmental stages of wheat. They found that some F-box genes were differentially expressed in vegetative and reproductive tissues, suggesting their specific roles in plant development. Similarly, mutations in the F-box gene *LARGER PANICLE* (*LP*) improved the panicle architecture and enhanced rice grain yield (Li *et al*., 2011). This suggests that the F-box domain-containing protein plays a vital role in regulating plant architecture, particularly panicle architecture and in the development of reproductive structures of plants as well.

3.4.4 Candidate Genes for the Level of Branching

Level of branching in cassava is a measure of flowering events that the plant has undergone (Fei *et al*., 2023; Pineda *et al*., 2020). The level of branching is a fundamental aspect of plant architecture that influences the plant's ability to capture light, distribute nutrients, overall biomass production and yield potential (Tang et al., 2019). The candidate genes identified from the significant SNPs for the level of branching influence branching in cassava as well as growth, and development. These genes likely contribute to the regulation of lateral shoot initiation and elongation, which in turn affects branching density and complexity.

At 6 and 9 months after planting, SNP S11_16097795 on chromosome 11 was observed to be correlated to level of branching. This shows the gene regulates the expression of two traits (pleiotropic effect). The candidate gene, Manes.11G089900, was identified within the range of this SNP. The function of this gene includes encoding Triosephosphate isomerase (TPI) (Aleksander *et al*., 2023). The effects of Triosephosphate isomerase (TPI) on crop plants are

not extensively understood. However, Chen & Thelen (2010) reported that the lack of a specific TPI isoform (pdTPI) has been shown to result in Arabidopsis thaliana plants that exhibit stunted growth and have abnormal chloroplasts which eventually limited their capability to transition into the reproductive stage. This suggests that TPI is crucial for average growth and development in plants.

Another SNP, S5_22148410, located on chromosome 5, was found to be related to the branching level at 9 months after planting. The gene that was identified in this domain is Manes.05G148900. This gene encodes cytokinin riboside 5'-monophosphate phosphoribohydrolase (Aleksander *et al*., 2023). One of the functions of cytokinin riboside 5'-monophosphate phosphoribohydrolase, an enzyme that is encoded by the *LONELY GUY* (*LOG*), its involvement in the last stage of cytokinin biosynthesis, which converts a cytokinin nucleotide to an active free-base form of cytokinins (Kurakawa *et al*., 2007). Loss of function mutations in the *LOG* gene caused abnormal branching patterns and decreased panicle size in rice plants (Kurakawa *et al*., 2007). Kuroha *et al*. (2009) reported the impact of the *LOG* genes on *Arabidopsis thaliana* and reported that plants with mutant *LOG* genes exhibited defective shoot growth at the reproductive stages. In contrast, the growth of adventitious roots was significantly enhanced in others, while some produced semi-dwarf plants with fewer flowers. Another gene found in the domain of this SNP, S5_22148410, is Manes.05G148800, which encodes the enzyme called endoglucanase (Aleksander *et al*., 2023). The endoglucanase gene breaks down cellulose, an essential component of plant cell walls. Perrot *et al.* (2022) highlighted the roles of plant β-glucanases in the hydrolysis of β-glucosidic linkages found in the structure of polysaccharides in the cell walls of plants and microbes and reported that the enzymes' catalytic activities underscore their crucial roles in plant growth, development, and environmental interaction.

The gene with the following identity: Manes.05G148700, was retrieved from the domain of the SNP, S5_22148410. This gene encodes Myb/SANT-like domain-containing protein (Aleksander *et al*., 2023). Roy (2015) discovered that the transcription factor Myb/SANT-like domain-containing protein regulates plant response to abiotic stress. According to Lee et al. (2009), MYB-domain transcription factors are products of the functions of the *LOF1* and *LOF2* genes in Arabidopsis: MYBs are expressed in the boundaries of plant organs, and their functions include the formation of axillary meristem and the separation of lateral organs in the shoot.

3.4.5 Candidate Genes for Harvest Index

Harvest index is a crucial determinant of yield efficiency in crop plants. It reflects the partitioning of biomass between harvested organs and total plant biomass. Harvest index is affected by various factors, such as sink-source dynamics, carbohydrate metabolism, and resource allocation (Hay, 2008; Smith *et al*., 2018).

Findings of the current study revealed a couple of SNPs and candidate genes that are associated with the harvest index. Among the candidate genes, were three genes that encode enzymes or proteins that are likely to regulate harvest index, indicating their involvement in optimizing resource allocation for maximal yield. These candidate genes include Manes.09G018900, identified within the range of the significant SNP, S9_3493565, on chromosome 9. This gene encodes glycosyltransferases (Aleksander *et al*., 2023). In plants, glycosyltransferases have diverse functions, which include modulation of stress tolerance and seed germination in rice (Wang *et al*., 2020). It is being associated with the regulation of anthocyanin content in plants and to substantially impact plant growth and development (Yao *et al*., 2019) in Tartary buckwheat. In Tartary buckwheat, the overexpression of glycosyltransferase genes increased yield and accelerated shoot and root growth (Yao *et al*., 2019).

Another SNP, S12_29499402, on chromosome 12 was found to be linked to the harvest index. The gene Manes.12G109600 which encodes *RING* (*Really Interesting New Gene*) -type E3 ubiquitin transferase (Aleksander *et al*., 2023) co-localized with this SNP. A study conducted by Yan *et al*. (2022) demonstrated that the loss-of-function mutation of the *Plant Architecture and Grain Number 1* (*PAGN1*) gene, a gene that belongs to the *RING_Ubox* (*RING (Really Interesting New Gene) finger domain and U-box domain*) superfamily, has a significant effect on plant architecture and yield in rice. The *PAGN1* mutant rice plants had higher plant height, number of tillers and grains per panicle, culminating in higher grain yield (Yan *et al*., 2022). A similar result was reported by Song *et al*. (2007), who found that a loss-of-function mutation in the rice gene encoding RING-type E3 ubiquitin ligases increased grain width, grain weight and yield during milking stage and producing larger spikelet hull.

SNP, S16_22907596, identified on chromosome 16 in proximity with the gene Manes.16G062600, which encodes JmjC-domain-containing protein (Aleksander *et al*., 2023). Shi *et al*. (2023) reported that the JmjC genes are responsible for accelerated shoot growth in the Moso bamboo (*Phyllostachys edulis*). Zhang *et al*. (2020) revealed that JmjC genes were overexpressed at the fibre-producing stage of the allotetraploid cotton species *Gossypium hirsutum*. This suggests that the JmjC genes are crucial to fibre development in cotton. The

functions of the JmjC genes were extensively highlighted by Yamaguchi (2021); based on the authors' submission, the level of expression of these genes could be influenced by the developmental stage of the crop as well as environmental factors. Sun & Zhou (2008) reported that the loss-of-function mutations of the JmjC genes significantly impact floral morphology and spikelet development in rice.

3.5 Conclusions:

Out of the 54,574 high density SNP markers used for this study, 17 significant SNPs were found to be associated with plant architecture and yield traits in cassava. Thirteen of these significant SNPs were linked to putative candidate genes for seven traits. A total of 18 putative candidate genes were identified for the seven traits including angle of branching (4), plant type (4), overall plant appearance (2), level of branching (4), harvest index (3), and number of harvested plants (1). These candidate genes exhibit various functions in relation to plant architecture, adaptation, yield, plant growth, development, stress response, and starch metabolism. Out of the 18 putative candidate genes identified in this study, one novel gene (Manes.01G077900) was discovered. This represents a significant contribution to knowledge. The findings of this study would provide a gateway into the exploration of the genetic control of cassava plant architecture and yield. This research output will provide cassava breeders with the genetic and molecular leverage required to fast-track cassava improvement for yield, productivity, and adaptation for mechanized cultivation and industrial use.

CHAPTER FOUR

4.0 VALIDATION OF HIGH THROUGHPUT PHENOTYPING PROTOCOL FOR ESTIMATING STARCH AND DRY MATTER CONTENT IN CASSAVA (*MANIHOT ESCULENTA*), USING NEAR-INFRARED REFLECTANCE SPECTROSCOPY (NIRS).

4.1 Introduction

Cassava (*Manihot esculenta* Crantz) has become a significant industrial crop (Nweke, 2005; Parmar *et al*., 2017). With a compound annual growth rate of 5.63%, the global starch industry is expected to grow from 78.4 billion dollars in 2022 to nearly $87.03 billion by 2029 (MMR, 2023). Nigeria, the world's largest producer of cassava, has the potential to tap into this lucrative market (Knoema, 2023). Thailand and Brazil have successfully transitioned from domestic use of cassava to an industrial crop (Felipe, 2018; Sowcharoensuk, 2020), generating 3.8 billion US dollars from the exports of cassava-based derivatives (Chriv, 2023). However, Nigeria's low market access is due to its subsistence-based production system (Ceballos *et al*., 2010). To ensure a constant supply of fresh cassava roots for both domestic and industrial consumption, cassava breeders in Nigeria should develop more cassava varieties with high starch and dry matter content and enhanced suitability for mechanized cultivation and harvesting (Ospina *et al*., 2002; Agbaji, 2022). Breeding for an important trait like starch and dry matter content in cassava can be a cumbersome process due to the conventional approach (gravimetric analysis) of estimating the starch and dry matter content of fresh cassava roots; the gravimetric analysis must be performed in a laboratory setting, which is quite tedious, time-consuming, and expensive.

The use of Near-infrared Reflectance Spectroscopy (NIRS) however, offers the possibility of a considerably less costly, simpler, and time-saving method for determining the starch and dry matter content in fresh cassava roots (Bantadjan *et al*., 2020; Maraphum, Saengprachatanarug, Wongpichet, *et al*., 2020; Nkouaya Mbanjo *et al*., 2022; Posom & Maraphum, 2023).

Near-infrared Reflectance Spectroscopy (NIRS) is an analytical technique that determines the chemical composition and physical properties of a sample based on its interaction with near-infrared light. The principle underlying the application of NIRs is that different molecules absorb light at certain wavelengths, and this gives rise to unique spectral fingerprints. NIRS uses a light source that emits radiation in the near-infrared range, typically

between visible light (780 nm) and the mid-infrared region (2500 nm) (Osibanjo *et al*., 2013; Beć *et al*., 2020; Kinhal, 2022). Molecules vibrate and rotate at specific frequencies. When NIRS light interacts with a sample, certain molecules absorb specific wavelengths of NIRS light corresponding to their vibrational and rotational energy levels. This unique pattern of absorption and reflection of each molecule at different wavelengths constistutes its spectral fingerprint. By analyzing the spectrum of NIRS light that passes through or reflected from a sample, we can identify and quantify the chemical composition and physical properties in the sample (Osibanjo *et al*., 2013; Beć *et al*., 2020). NIRS offers a rapid, non-destructive, and cost-effective phenotyping protocol for estimating essential crop traits, thereby aiding their improvement through accurate and accelerated selection (Kinhal, 2022).

Near-infrared Reflectance Spectroscopy (NIRS) technology has been evaluated for several purposes, including quantification of nutrient contents in food crops (grains, roots, and tubers), (Montes *et al*., 2013; García-sánchez, 2015; Johnson & Walsh, 2020), assessing dry matter content and cyanogenic potential (Sánchez *et al*., 2014), starch content (Maraphum, Saengprachatanarug, & Wongpichet, 2020), beta carotene and total carotenoid content in cassava (Ikeogu *et al*., 2019) as well as estimating texture and cooking time of common beans (Wafula *et al*., 2020). This technology has also been used in in-vivo estimation of chlorophyll contents in leaves (Li *et al*., 2019). NIRS has also been used in selecting rice seed mutants from a seed lot exposed to mutagenic treatments (Jankowicz-Cieslak *et al*., 2016).

The rate at which improved cassava varieties with high and top-quality starch content and dry matter content are being developed will increase as portable, precise, quick, high-throughput starch and dry matter assessment equipment that utilises NIRS becomes more readily available. Fresh cassava roots' starch and dry matter contents have been assessed using NIRS, and the derived calibration equation was able to predict starch and dry matter content with accuracy (Bantadjan *et al*., 2020). A couple of spectrometers, ASD QualitySpec® Trek (QST) (350-2500 nm) benchtop FOSS XDS Rapid Content™ Analyzer (400-2490 nm), with wavelengths that capture the spectra information within the NIR range (780-2500 nm), are being used for spectra data collection for the development of prediction models and estimation of starch and dry matter content in fresh cassava roots (Abincha *et al*., 2021; Posom & Maraphum, 2023). These two devices are quite expensive and could not be afforded by breeders in the universities or national research institutes who operate on low budgets (Profcontrol, 2024). However, a new, affordable, portable spectrometer; SCiO sensor spectrometer (740 to 1070 nm) has been introduced for the estimation of starch content and dry matter content in fresh cassava roots. The narrow wavelengths coverage (740 to 1070 nm) of the SCiO sensor spectrometer has

generated a lot of questions and cast doubt on its use in terms of its accuracy of prediction. Nkouaya Mbanjo *et al*. (2022) made extensive comparisons among the three spectrometers; ASD QualitySpec®, FOSS XDS Rapid Content™ Analyzer and the SCiO sensor spectrometer and observed that the SCiO sensor spectrometer had the best predictive accuracy among the devices despite its restricted spectral range.

The handheld SCiO sensor spectrometer was used for this research to validate the findings of (Nkouaya Mbanjo *et al*., 2022) on different cassava accessions and across different environments.

The objectives of this study were to evaluate starch and dry matter content in fresh cassava roots using NIRS technique and to assess the consistency and accuracy of the NIRS data obtained with the SCiO sensor spectrometer in evaluating starch and dry matter content in fresh cassava roots.

4.2 Materials and Methods

4.2.1 Plant Materials

The 453 cassava accessions used for these trials were at the Preliminary Yield Trial (PYT) stage of the cassava breeding program. These included 448 accessions advanced from the clonal evaluation trial and five commercial varieties which were used as checks. The details of the accessions, including those of the crosses/parents used and the commercial checks are contained in (Table 3.1) of the supplementary file. The trials were conducted in two locations (Table 4.1) in Nigeria across three planting seasons (2019/2020, 2020/2021, and 2021/2022). Two trials were evaluated in Ikenne in the 2019/2020 and 2020/2021 planting seasons, while the single trial in Ibadan was evaluated in the 2021/2022 planting season. The number of accessions extracted from the Ikenne trial in the 2019/2020 planting season for NIRs calibration and validation model development were 174, including five commercial varieties used as checks, while for the trial conducted in the 2020/2021 planting season, 259 accessions including five check varieties were used. Lastly, for the trial evaluated at Ibadan in the 2021/2022 planting season, 272 accessions including five commercial varieties used as checks were planted. Two of the accessions planted in the Ikeenne trial in 2019/2020 were removed during data cleaning, while the remaining 172 accessions were used for the calibration and validation of the NIRs model.

The trials would be referred to as follows: Trial A (the Ikene trial in the 2019/2020 planting season), Trial B (the Ikene trial in the 2020/2021 planting season) and Trial C (the Ibadan trial

in the 2021/2022 planting season). The trial was laid out in a modified augmented block design with two replications per environment (location x season). Genotypes were assigned to incomplete blocks nested within replicates to control for field heterogeneity. The field layout contained both row and column coordinates, which allowed spatial modelling to account for possible field trends. Two to three commercial check varieties were included in each block to provide benchmarks for performance comparison and quality control. A plot comprises three rows with three plants planted on ridges per row. A spacing of 1.0 m was maintained between ridges, while a spacing of 0.8 m was observed within plants in a row.

The accessions used for NIRs model development in trial A were selected based on their high fresh root yield, high dry matter and starch content while the accessions selected for the development of NIRs model in trial B entail accessions with extreme values (highest and lowest) with respect to fresh root yield, dry matter content and starch content. This was done to enhance the robustness of the data collected from this trial. The accessions used in trial C were selected based on high fresh root yield, dry matter content and starch content.

Table 4.1 | The coordinates and weather data for the trial locations in Nigeria

Location	GIS Coordinates	Altitude (MASL)	Average Rainfall (mm)	Average Temperature (°C)	Agroecological Zone
Ikenne	Lat 6.8718° N, Long 3.7106° E	90	2,000	27	Humid Forest
Ibadan	Lat 7.4946° N, Long 3.9003° E	188	1,800	29	Derived Savannah

MASL – Meters Above Sea Level, mm – Milimeters, °C – Degree Celcius

4.2.2 Preparation of Cassava Roots for Starch Extraction

Six fresh cassava roots of each accession were selected per plot from the total harvested roots after weighing the overall fresh roots per plot. Cassava roots of different sizes were selected at random. The selected roots were healthy, intact, rot-free and deterioration-free. The roots were labelled and transported to the laboratory in sampling bags. The protocol described by Nkouaya Mbanjo *et al*. (2022) was used in extracting starch from the fresh cassava roots. The fresh cassava roots were thoroughly washed, peeled and the two extreme ends were cut off. The remaining part of the roots were shredded at both ends and at the middle, using a hand grater with 3-mm hole diameter. The shredded samples were thoroughly mixed. One hundred grams of the thoroughly mixed shredded samples were weighed and transferred into a blender. Two hundred millilitres of water was added to the shredded samples and blended for one minute. The blended samples were diluted with two litres of water and filtered using a 180mm mesh size sieve. To allow the starch granules to settle, the mixture was left at room temperature for three hours. The starch residue was air-dried for 72 hours at ambient temperature for 24 hours at 40°C in the oven after the supernatant was properly decanted. The fresh cassava root's starch content (SC), which is determined by weighing the dry sediments, is represented as a percentage of the fresh root yield. The starch content was calculated using the following formula:

$$SC\ (\%) = \frac{DSM}{FM} X\ 100$$

The fresh root mass (FM) represents the weight of the root matter, whereas the dry starch mass (DSM) represents the weight of starch recovered from a known weight of the root matter.

4.2.3 Collection of Spectra Data

4.2.3.1 Spectra Data Collection with Portable Hand-held Spectrometer (SCiO™)

The spectra data were collected within the near infrared (NIR) region of 740 to 1070 nm with a resolution of 1 nm using the pocket-sized spectrometer SCiO™, a molecular sensor made by Consumer Physics, Tel Aviv, Israel. The SCiO smartphone app automatically uploaded the spectrum data that the SCiO sensor had recorded to the SCiO cloud storage. The data-collecting tablet was using Bluetooth to connect to the SCiO sensor through the downloaded SCiO smartphone App.

The SCiO sensor was calibrated with the aid of the inbuilt standardization reference in the SCiO case prior to spectra data collection. The samples used for spectra data were prepared in a similar fashion with the samples used for starch extraction for the reference data. The shredded fresh cassava roots were adequately mixed and were placed in quartz cell glasses. With the optical head pointing downward, the SCiO optical shade was positioned atop the cell quartz and attached to the sensor. The light source lighted the shredded cassava samples in the quartz cell, and the sensor recorded the reflected spectrum data, which was then uploaded to the SCiO cloud storage website. Spectra data were collected from each cassava accession in three technical replicates, meaning three representative samples from the fresh cassava roots were used per each cassava accession. Three spectra scan was performed on each of the technical replicates by rotating the quartz cells in different direction to capture the spectra data in three different dimensions. The completed spectra data was downloaded from the SCiO cloud storage for analyses. The average values of the repeated scans per sample were used for data analyses.

4.2.4 Reference (Starch and Dry Matter Content) data analysis

The reference data constitute the starch content and dry matter content data obtained through the laboratory gravimetric procedure. The reference data was analysed with the linear mixed model fitted as follows, using the lmer function from the lme4 package (Bates *et al.*, 2015) of the R software (R Core Team, 2020).

$$\eta_{ijklm} = \mu + \alpha_i + \beta_{ij} + \gamma_k + \delta_{ik} + \epsilon_{ijl} + e_{ijkl}$$

Where η_{ijklm} is the yield value for the m^{th} plot in the l^{th} block of the j^{th} replicate of the i^{th} environment for the k^{th} accession; μ is the overall mean; α_i is the fixed effect of the i^{th} environment; β_{ij} is the fixed effect of the interaction between the i^{th} environment and the j^{th} replicate; γ_k is the random effect of the k^{th} accession; δ_{ik} is the random effect of the interaction between the i^{th} environment and the k^{th} accession; ϵ_{ijl} is the random effect of the interaction between the i^{th} environment, the j^{th} replicate, and the l^{th} block; and e_{ijkl} is the random residual error.

The random effects γ_k, δ_{ik}, and ϵ_{ijl} are assumed to be independent and normally distributed with mean of zero and variance components σ^2a, σ^2ea, and σ^2b, respectively. The residual error e_{ijkl}

is also assumed to be independent and normally distributed with mean of zero and variance component $\sigma^2 e$.

The best linear unbiased prediction (BLUP) values derived from this model were used as pooled phenotypic values across environments. The broad sense heritability (H^2) values were calculated as follows:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e^2}{er}}$$

Where H^2 is the broad sense heritability estimate, $\sigma^2 g$ is the genetic variance component of the accession effect, $\sigma^2 ge$ is the variance component of the genotype by environment effect, $\sigma^2 e$ is the variance component of the residual error, e is the number of environments and r is the number of replicates.

The estimation of genetic advance as a percentage of mean (GAM) was performed using the formula described in (Johnson *et al.*, 1955).

$$GAM = \frac{K \times \sigma_p \times H}{100}$$

Where:

K = 2.06 at 5% selection intensity.

H = Heritability.

σp = Phenotypic standard deviation.

4.2.5 Spectra data analysis

Prior to the calibration and the validation of the models developed for this trial, the raw data were subjected to mathematical pre-treatments.

According to Huang *et al.* (2010), pre-treatment of spectral data comes with a lot of benefits amongst which are the minimization of unwanted variations (baseline offsets and multiplicative effects), reduction of noise as well as preservation of the integrity of the signal of interest. In addition to these, Xu *et al.* (2022) stated that pre-treatment of spectra data enhances the visualization of spectra signature. The authors also highlighted instrumental and experimental artifacts as sources of unwanted variations. Pre-treatment of spectra data also aids in correcting

for baseline and background shifts so as to uncover hidden information thereby increasing spectra resolution (Metrohm, 2021). Above all, pre-treatment of spectra data improves model performance (Huang *et al*., 2010).

The R package Waves version 0.2.4 Hershberger *et al*. (2021) was used in performing data pre-treatment, model development and validation. Thirteen pre-treatment options were made available in the Waves package. These include no treatment option and a total of twelve mathematical pre-treatment algorithms. The pre-treatment options that are embedded in the waves package are herein stated: Raw data (no pre-treatment is applied), Standard normal variate (SNV), SNV and first derivative, SNV and second derivative, First derivative, Second derivative, Savitzky–Golay filter (SG), Standard normal variate and Savitzky–Golay filter (SNV and SG), Gap segment derivative (window size = 11), SG and first derivative (window size = 5), SG and first derivative (window size = 11), SG and second derivative (window size = 5), and SG and second derivative (window size = 11). All the pre-treatment options were used on the data prior to model development. The partial least square regression model (PLSR) was used for model development and the internal cross validation scheme was deployed to divide the genotypes into two viz; calibration (training set) and validation (test set). The internal cross validation scheme randomly grouped the dataset into calibration and validation sets. The calibration sets contained 70% of the genotypes while the remaining 30% of the genotypes constituted the validation set. In addition to this, the model with the best prediction ability was identified by setting the cross-validation at the five-fold levels. The number of iterations was set at (niter = 50), thereby repeating the process 50 times. The following key statistical parameters were used in evaluating the model performance: Root mean squared error of prediction (RMSEp), Squared Pearson's correlation between predicted and observed test set values (R^2p), Ratio of standard deviation of observed test set values to RMSEp (RPD), Ratio of performance to interquartile difference (RPIQ), Concordance correlation coefficient (CCC), Average difference between the predicted and observed values (Bias), Standard error of prediction (SEP), Root mean squared error of cross-validation (RMSEcv), Coefficient of multiple determination of cross-validation for PLS models (R^2cv), Squared Spearman's rank correlation between predicted and observed test set values (R^2sp), and Best number of components in a PLS model (best.ncomp).

4.3 Results

The error variance was lower than the genotypic variance for both dry matter and starch content (Table 4.2). High values (0.83 & 0.75) of broad sense heritability were obtained for both starch and dry matter content respectively. The phenotypic and genotypic coefficient of variation values of 12.32% and 10.67% were obtained for starch content while lesser values of 9.76% and 8.87% were obtained for dry matter content. The higher value for genetic advance as a percentage of mean 19.07 was realized from starch content compared to 16.66 obtained from dry matter content.

Table 4.2 | Estimates of variance components, broad sense heritability, PCV, GCV, and genetic advance for dry matter and starch content for all the cassava accessions evaluated across three environments in Nigeria.

Trait	Mean	σ^2_g	σ^2_{GxE}	σ^2_e	H^2	PCV(%)	GCV(%)	GA	GAM
Starch Content	28	8.92	1.11	1.87	0.75	12.32	10.67	5.34	19.07
Dry Matter Content	36	10.2	0.71	1.42	0.83	9.76	8.87	6	16.66

H^2 - broad sense heritability, GA - Genetic advance, GAM - genetic advance as a percentage of mean, σ^2e – residual variance, PCV, phenotypic coefficient of variation, σ^2p – phenotypic variance, GCV- genotypic coefficient of variation, σ^2g – genotypic variance.

The R^2p values (Table 4.5), important indicator in assessing the accuracy of prediction of the partial least squares regression (PLSR) model ranged from 0.60 to 0.62. The R^2sp values on the other hand had values from 0.54 and 0.57. The RPD and RPIQ values ranged from 1.58 to 1.63 and 1.86 to 1.92 respectively. The CCC value was between 0.75 and 0.76. While the bias was as low as -0.02 with the maximum value being 0.00 and the SEP values were between 2.15 and 2.22.

The results in (Table 4.6) shows that the PLS models were able to estimate the dry matter content of fresh cassava roots with moderate accuracy and precision. The R^2p values ranged from 0.68 to 0.70, the R^2sp values were similar to the R^2p values which were between 0.68 and 0.69. The RPD and RPIQ values ranged from 1.76 to 1.83 and 2.20 to 2.9 respectively. The CCC values ranged from 0.81 to 0.82. The bias and SEP values were low for all pre-treatments with values ranging from -0.04 to -0.02 and 2.26 and 2.35 respectively.

In the same vein, the accuracy of the PLSR model in predicting the performance of starch content from trial B is shown in (Table 4.7). The R^2p values ranged from 0.78 to 0.80. The R^2sp values were similar to the minimum value of 0.77 and the maximum value of 0.79. The RPD and RPIQ values ranged from 2.17 to 2.27 and 2.68 to 2.81 respectively. There was a slight difference in the values of CCC across the pre-treatments which ranged from 0.88 to 0.89. While the bias and SEP values were low for all pre-treatments with values that are less than 0.03 and 2.15 respectively.

The performance of the PLSR model in predicting the performance of dry matter content from trial B is shown in (Table 4.8). The R^2p values ranged from 0.78 to 0.79. The R^2sp values were similar to the R^2p values with the minimum value of 0.75 and the maximum value of 0.77. The RPD and RPIQ values ranged from 2.14 to 2.19 and 2.78 to 2.85 respectively. The uniform CCC value of 0.88 was observed across board for all the pre-treatments. While the bias and SEP values were low for all models with values that are less than 0.04 and 2.46 respectively.

The results also showed that the pre-treatment methods had little effect on the model performance. The differences among the models with different pre-treatment methods were negligible in terms of the statistical parameters. The best model was obtained with the D2 pre-treatment method, which performed slightly better than the other methods in terms of RMSEp, R^2p, RPD, RPIQ, and CCC. The worst model was obtained with the SGD1 pre-treatment method, which performed slightly worse than the other methods in terms of bias and best.ncomp.

Table 4.3 | Effect of different spectral pretreatments on the prediction accuracy of starch content in fresh cassava roots from Trial A

Pretreatment	RMSEp	R^2p	RPD	RPIQ	CCC	Bias	SEP	RMSEcv	R^2cv	R^2sp	best.ncomp
SNV1D	2.14	0.62	1.63	1.92	0.76	0	2.15	2.05	0.64	0.57	3.68
SNV2D	2.16	0.62	1.61	1.9	0.76	-0.02	2.17	2.01	0.66	0.56	4.04
SNV	2.16	0.62	1.62	1.9	0.76	-0.01	2.17	2.04	0.65	0.57	5.04
SNVSG	2.16	0.62	1.61	1.9	0.76	-0.01	2.17	2.04	0.65	0.57	4.8
SGD1	2.16	0.61	1.61	1.9	0.76	-0.01	2.17	2.05	0.64	0.56	4.58
SG.D1W11	2.16	0.61	1.61	1.9	0.76	-0.02	2.18	2.04	0.65	0.55	4.54
D1	2.17	0.61	1.61	1.89	0.76	-0.02	2.18	2.01	0.65	0.55	4.98
Raw_data	2.17	0.61	1.61	1.9	0.76	-0.01	2.18	2.06	0.64	0.56	6.16
SG.D1W5	2.17	0.61	1.61	1.89	0.76	-0.02	2.18	2.02	0.65	0.55	4.84
SG	2.17	0.61	1.61	1.9	0.76	0	2.18	2.05	0.64	0.56	6
SG.D2W11	2.19	0.6	1.59	1.87	0.76	-0.01	2.21	2	0.66	0.55	4.56
SG.D2W5	2.2	0.6	1.58	1.86	0.75	-0.01	2.21	2	0.66	0.55	5.14
D2	2.21	0.6	1.58	1.86	0.75	-0.01	2.22	2	0.66	0.54	5.18

RMSEp: Root mean squared error of prediction, R^2p: Squared Pearson's correlation between predicted and observed test set values, RPD: Ratio of standard deviation of observed test set values to RMSEp, RPIQ: Ratio of performance to interquartile difference, CCC: Concordance correlation coefficient, Bias: Average difference between the predicted and observed values, SEP: Standard error of prediction, RMSEcv: Root mean squared error of cross-validation, R^2cv : Coefficient of multiple determination of cross-validation for PLS models, R^2sp: Squared Spearman's rank correlation between predicted and observed test set values, and best.ncomp: Best number of components in a PLS model.

Raw_data : Raw data, SNV : Standard normal variate, SNV1D: SNV and first derivative, SNV2D: SNV and second derivative, D1: First derivative, D2: Second derivative, SG: Savitzky–Golay filter, SNVSG: Standard normal variate and Savitzky–Golay filter, SGD1: Gap segment derivative (window size = 11), SG.D1W5: SG and first derivative (window size = 5), SG.D1W11: SG and first derivative (window size = 11), SG.D2W5: SG and second derivative (window size = 5), and SG.D2W11: SG and second derivative (window size = 11)

Table 4.4 | Effect of different spectral pretreatments on the prediction accuracy of dry matter content in fresh cassava roots from Trial A

Pretreatment	RMSEp	R^2p	RPD	RPIQ	CCC	Bias	SEP	RMSEcv	R^2cv	R^2sp	best.ncomp
SNV1D	2.24	0.7	1.83	2.29	0.82	-0.02	2.26	2.09	0.74	0.69	6.02
SNV2D	2.26	0.7	1.82	2.27	0.82	-0.03	2.27	2.13	0.73	0.69	3.94
SNV	2.27	0.7	1.81	2.26	0.82	-0.04	2.28	2.09	0.74	0.69	8.16
SG.D2W11	2.28	0.69	1.8	2.26	0.82	-0.02	2.29	2.12	0.73	0.69	4.54
SNVSG	2.28	0.69	1.8	2.25	0.82	-0.05	2.29	2.1	0.73	0.69	8.04
SG.D1W5	2.29	0.69	1.79	2.24	0.82	-0.02	2.31	2.1	0.73	0.68	6.36
SGD1	2.3	0.69	1.79	2.24	0.82	-0.03	2.31	2.13	0.73	0.69	7.78
Raw_data	2.3	0.69	1.78	2.23	0.81	-0.03	2.32	2.12	0.73	0.68	9.52
D1	2.3	0.69	1.78	2.23	0.81	-0.02	2.32	2.1	0.73	0.68	6.3
SG	2.31	0.69	1.78	2.23	0.81	-0.03	2.32	2.12	0.73	0.68	9.56
SG.D1W11	2.31	0.69	1.78	2.22	0.81	-0.04	2.32	2.1	0.73	0.69	6.7
SG.D2W5	2.32	0.68	1.77	2.21	0.81	-0.03	2.34	2.16	0.72	0.68	4.3
D2	2.33	0.68	1.76	2.2	0.81	-0.03	2.35	2.15	0.72	0.68	4.36

RMSEp: Root mean squared error of prediction, R^2p: Squared Pearson's correlation between predicted and observed test set values, RPD: Ratio of standard deviation of observed test set values to RMSEp, RPIQ: Ratio of performance to interquartile difference, CCC: Concordance correlation coefficient, Bias: Average difference between the predicted and observed values, SEP: Standard error of prediction, RMSEcv: Root mean squared error of cross-validation, R^2cv : Coefficient of multiple determination of cross-validation for PLS models, R^2sp: Squared Spearman's rank correlation between predicted and observed test set values, and best.ncomp: Best number of components in a PLS model.

Raw_data : Raw data, SNV : Standard normal variate, SNV1D: SNV and first derivative, SNV2D: SNV and second derivative, D1: First derivative, D2: Second derivative, SG: Savitzky–Golay filter, SNVSG: Standard normal variate and Savitzky–Golay filter, SGD1: Gap segment derivative (window size = 11), SG.D1W5: SG and first derivative (window size = 5), SG.D1W11: SG and first derivative (window size = 11), SG.D2W5: SG and second derivative (window size = 5), and SG.D2W11: SG and second derivative (window size = 11)

Table 4.5| Comparing the effects of different spectral pretreatments on the prediction accuracy of starch content in fresh cassava roots from Trial B

Pretreatment	RMSEp	R^2p	RPD	RPIQ	CCC	Bias	SEP	RMSEcv	R^2cv	R^2sp	best.ncomp
SG	2.1	0.8	2.27	2.81	0.89	0.01	2.1	1.93	0.83	0.79	13.52
SG.D1W11	2.1	0.8	2.27	2.8	0.89	0.02	2.11	1.93	0.83	0.78	9.3
Raw_data	2.1	0.8	2.27	2.8	0.89	0	2.11	1.93	0.83	0.78	13.7
SGD1	2.11	0.8	2.26	2.79	0.89	0.01	2.12	1.95	0.83	0.78	13.74
SNV	2.11	0.8	2.25	2.78	0.89	0.01	2.12	1.92	0.83	0.79	13.16
D1	2.11	0.8	2.26	2.79	0.89	0.01	2.12	1.93	0.83	0.78	8.7
SG.D1W5	2.11	0.8	2.26	2.79	0.89	0.02	2.12	1.94	0.83	0.78	8.4
SNVSG	2.12	0.8	2.24	2.77	0.89	0.01	2.13	1.93	0.83	0.78	12.78
SG.D2W11	2.12	0.8	2.25	2.77	0.89	0.02	2.13	1.91	0.84	0.78	10.28
SG.D2W5	2.13	0.8	2.24	2.77	0.89	0.02	2.13	1.91	0.84	0.78	10.98
D2	2.13	0.8	2.24	2.76	0.89	0.03	2.14	1.91	0.84	0.78	10.96
SNV1D	2.14	0.79	2.22	2.75	0.89	0	2.15	1.94	0.83	0.78	9.06
SNV2D	2.2	0.78	2.17	2.68	0.88	0.01	2.2	1.92	0.83	0.77	12.58

RMSEp: Root mean squared error of prediction, R^2p: Squared Pearson's correlation between predicted and observed test set values, RPD: Ratio of standard deviation of observed test set values to RMSEp, RPIQ: Ratio of performance to interquartile difference, CCC: Concordance correlation coefficient, Bias: Average difference between the predicted and observed values, SEP: Standard error of prediction, RMSEcv: Root mean squared error of cross-validation, R^2cv : Coefficient of multiple determination of cross-validation for PLS models, R^2sp: Squared Spearman's rank correlation between predicted and observed test set values, and best.ncomp: Best number of components in a PLS model.

Raw_data : Raw data, SNV : Standard normal variate, SNV1D: SNV and first derivative, SNV2D: SNV and second derivative, D1: First derivative, D2: Second derivative, SG: Savitzky–Golay filter, SNVSG: Standard normal variate and Savitzky–Golay filter, SGD1: Gap segment derivative (window size = 11), SG.D1W5: SG and first derivative (window size = 5), SG.D1W11: SG and first derivative (window size = 11), SG.D2W5: SG and second derivative (window size = 5), and SG.D2W11: SG and second derivative (window size = 11)

Table 4.6| Effect of different spectral pretreatments on the prediction accuracy of dry matter content in fresh cassava roots from Trial B

Pretreatment	RMSEp	R^2p	RPD	RPIQ	CCC	Bias	SEP	RMSEcv	R^2cv	R^2sp	best.ncomp
D2	2.4	0.79	2.19	2.85	0.88	0.03	2.41	2.16	0.83	0.77	10.34
SG.D2W5	2.4	0.79	2.18	2.84	0.88	0.02	2.41	2.16	0.83	0.76	10.24
SNV2D	2.42	0.79	2.17	2.83	0.88	0.03	2.42	2.17	0.82	0.76	10.7
SG.D2W11	2.43	0.79	2.16	2.81	0.88	0.02	2.44	2.18	0.82	0.76	10.12
Raw_data	2.43	0.78	2.16	2.81	0.88	0.02	2.44	2.29	0.8	0.76	9.68
SG	2.43	0.78	2.16	2.81	0.88	0.02	2.44	2.28	0.8	0.76	10.12
SNV	2.44	0.78	2.15	2.8	0.88	0.02	2.45	2.32	0.8	0.76	6.88
SNVSG	2.44	0.78	2.15	2.8	0.88	0.02	2.45	2.32	0.8	0.76	6.84
D1	2.44	0.78	2.15	2.79	0.88	0.02	2.45	2.24	0.81	0.76	7.62
SG.D1W11	2.45	0.78	2.14	2.79	0.88	0.02	2.46	2.26	0.81	0.75	7.8
SG.D1W5	2.45	0.78	2.14	2.79	0.88	0.02	2.46	2.24	0.81	0.75	7.8
SNV1D	2.45	0.78	2.14	2.79	0.88	0.02	2.46	2.26	0.81	0.75	7.38
SGD1	2.45	0.78	2.14	2.78	0.88	0.04	2.46	2.29	0.8	0.75	10.08

RMSEp: Root mean squared error of prediction, R^2p: Squared Pearson's correlation between predicted and observed test set values, RPD: Ratio of standard deviation of observed test set values to RMSEp, RPIQ: Ratio of performance to interquartile difference, CCC: Concordance correlation coefficient, Bias: Average difference between the predicted and observed values, SEP: Standard error of prediction, RMSEcv: Root mean squared error of cross-validation, R^2cv : Coefficient of multiple determination of cross-validation for PLS models, R^2sp: Squared Spearman's rank correlation between predicted and observed test set values, and best.ncomp: Best number of components in a PLS model.

Raw_data : Raw data, SNV : Standard normal variate, SNV1D: SNV and first derivative, SNV2D: SNV and second derivative, D1: First derivative, D2: Second derivative, SG: Savitzky–Golay filter, SNVSG: Standard normal variate and Savitzky–Golay filter, SGD1: Gap segment derivative (window size = 11), SG.D1W5: SG and first derivative (window size = 5), SG.D1W11: SG and first derivative (window size = 11), SG.D2W5: SG and second derivative (window size = 5), and SG.D2W11: SG and second derivative (window size = 11)

The prediction accuracy of the results obtained for estimating dry matter content from fresh cassava roots in trial C (Table 4.9) was higher than the values obtained from trial A but lower than those obtained from trial B. The results indicated that the RMSEp values were between 1.51 and 1.64, while R^2p values were as high as 0.74 with the lowest value being 0.70. Other parameters such as RPD and RPIQ have high values which were between 1.86 to 2.03 and 2.32 to 2.53 respectively. However, the CCC was as high as 0.85 with the lowest value of 0.82 while the bias and SEP were as high as 0.04 and 1.66 respectively.

Table 4.7| The statistics of parameters used in estimating the PLSR model performance in predicting dry matter content from trial C.

Pretreatment	RMSEp	R^2p	RPD	RPIQ	CCC	Bias	SEP	RMSEcv	R^2cv	R^2sp	best.ncomp
SNVSG	1.51	0.74	2.03	2.53	0.85	0.01	1.52	1.4	0.77	0.73	5
SNV	1.52	0.74	2.01	2.51	0.84	0.01	1.54	1.39	0.78	0.73	5.34
SGD1	1.54	0.73	1.98	2.47	0.84	0.03	1.56	1.38	0.78	0.72	5.84
SG	1.56	0.73	1.97	2.45	0.84	0.02	1.57	1.38	0.78	0.72	7.34
SG.D1W11	1.56	0.73	1.96	2.45	0.84	0.04	1.58	1.37	0.78	0.72	5.42
SNV1D	1.57	0.73	1.96	2.45	0.84	0.03	1.58	1.38	0.78	0.72	4.96
Raw_data	1.57	0.72	1.94	2.42	0.83	0.03	1.59	1.37	0.78	0.71	7.84
SG.D1W5	1.58	0.72	1.95	2.43	0.83	0.04	1.59	1.37	0.79	0.72	5.62
D1	1.58	0.72	1.95	2.43	0.83	0.03	1.6	1.35	0.79	0.72	5.94
SG.D2W11	1.58	0.72	1.94	2.42	0.83	0.02	1.6	1.32	0.8	0.72	6.04
SG.D2W5	1.6	0.72	1.91	2.38	0.83	0.02	1.62	1.32	0.8	0.71	6.8
D2	1.62	0.71	1.9	2.37	0.83	0.02	1.63	1.32	0.8	0.71	6.84
SNV2D	1.64	0.70	1.86	2.32	0.82	0.01	1.66	1.42	0.77	0.7	5.12

RMSEp: Root mean squared error of prediction, R^2p: Squared Pearson's correlation between predicted and observed test set values, RPD: Ratio of standard deviation of observed test set values to RMSEp, RPIQ: Ratio of performance to interquartile difference, CCC: Concordance correlation coefficient, Bias: Average difference between the predicted and observed values, SEP: Standard error of prediction, RMSEcv: Root mean squared error of cross-validation, R^2cv : Coefficient of multiple determination of cross-validation for PLS models, R^2sp: Squared Spearman's rank correlation between predicted and observed test set values, and best.ncomp: Best number of components in a PLS model.

Raw_data : Raw data, SNV : Standard normal variate, SNV1D: SNV and first derivative, SNV2D: SNV and second derivative, D1: First derivative, D2: Second derivative, SG: Savitzky–Golay filter, SNVSG: Standard normal variate and Savitzky–Golay filter, SGD1: Gap segment derivative (window size = 11), SG.D1W5: SG and first derivative (window size = 5), SG.D1W11: SG and first derivative (window size = 11), SG.D2W5: SG and second derivative (window size = 5), and SG.D2W11: SG and second derivative (window size = 11)

4.4 Discussion

The results indicate that there is a strong relationship between the starch contents and dry matter contents of the fresh cassava roots. This agrees with the findings of Peprah *et al*., (2020); Silva *et al*., (2023); Malai *et al*., (2024). This implies that both traits can be used in predicting each other and accurately used for selection purpose. The high broad sense heritability values observed among the accessions for starch content and dry matter content showed that the genotypic components strongly contributed to the variation observed for these traits and can therefore be improved in fresh cassava roots.

The Partial Least Squares Regression (PLSR) model demonstrated moderate accuracy and precision in predicting the starch and dry matter contents of fresh cassava roots from all the three trials. The R^2p values ranged from 0.60 to 0.80, indicating a moderate to strong relationship between the predicted and actual starch and dry matter content. Similarly, the R^2sp values, which ranged from 0.54 to 0.79, further confirmed the moderate to strong predictive ability of the model on an independent dataset. The RPD values, that ranged from 1.58 to 2.27, and RPIQ values, which ranged from 1.86 to 2.85, indicated that the model could predict starch and dry matter content with satisfactory accuracy and precision. The CCC values of 0.75 to 0.89 observed for all trials further highlight the model's strong predictive capability. Additionally, the relatively low bias and SEP values for all models, with values less than 0.04 and 2.46, respectively, suggest that the model's predictions were unbiased and accurate. These findings were corroborated by the work of Maraphum et al. (2022) who reported R^2p, RMSEp, and RPD of 0.75, 2.00, and 2.00, respectively for dry matter content in fresh cassava roots, and Malai et al. (2024) who reported R^2cal, R^2val, SEP, ratio of prediction to standard deviation (RPD) of 0.69, 0.66, 3.18%, and 1.81 for starch content and 0.63, 0.54, 4.15%, and 1.50, for dry matter content respectively.

Based on the results obtained for the prediction of starch content from fresh cassava roots in trial A, the SNV1D pre-treatment outperformed other pre-treatments in predicting the starch content with enhanced accuracy. The SNV1D pre-treatment yielded the lowest RMSEp (2.14), the highest R^2p (0.62), RPD (1.63), RPIQ (1.92), CCC (0.76), and R^2sp (0.57), as well as the smallest Bias (0.00) and SEP (2.15). The SNV1D pre-treatment also demonstrated the lowest RMSEcv (2.05) among all the pre-treatments, indicating that it effectively reduced noise and enhanced the signal in the spectra data. On the other hand, the other pre-treatments exhibited slightly inferior performance, with higher RMSEp, Bias, and SEP, and lower R^2p, RPD, RPIQ, CCC, and R^2sp. The D2 pre-treatment however, displayed the poorest

performance among all the pretreatments, with the highest RMSEp (2.21), Bias (-0.01), and SEP (2.22), and the lowest R^2p (0.60), RPD (1.58), RPIQ (1.86), CCC (0.75), and R^2sp (0.54). Therefore, the SNV1D pre-treatment is the most suitable for predicting starch content in fresh cassava roots using PLSR models based on spectra data obtained on fresh cassava roots from trial A, using a portable near-infrared spectrometer, as it demonstrated a clear advantage over the other pre-treatments in terms of various performance metrics, including RMSEp, R^2p, RPD, RPIQ, CCC, Bias, SEP, RMSEcv, and best.ncomp. Similar results were obtained by Nkouaya Mbanjo et al. (2022).

The results obtained for starch prediction in trial B, however, showed a sharp departure from the outcome of the trial A with respect to the impact of the pre-treatments on the accuracy of prediction. The results revealed that the SG pre-treatment demonstrated superior performance among all the pre-treatments. It achieved the lowest RMSEp (2.10), the highest R^2p (0.80), RPD (2.27), RPIQ (2.81), CCC (0.89), and R^2cv (0.83), as well as the smallest Bias (0.01) and SEP (2.10). The optimal number of latent variables for the PLSR model under the SG pre-treatment was approximately 14, as indicated by the best.ncomp value of 13.52. The SG pre-treatment also had the lowest RMSEcv (1.93) among all the pre-treatments, suggesting its effectiveness in reducing noise and enhancing the signal in the spectra data. The R^2sp for the SG pre-treatment was 0.79, indicating that the SG pre-treatment preserved the spectral information well. Similar results were reported by Nkouaya Mbanjo et al. (2022) on data collected from two separate trials that were conducted in the same location, and the same planting season but on cassava accessions that were at different breeding stage (uniform yield trial and advanced yield trial stage).

The SG.D1W11 pre-treatment showed a similar performance to the SG pre-treatment, with identical values for RMSEp (2.10), R2p (0.80), RPD (2.27), and RPIQ (2.80), and slightly higher values for Bias (0.02) and SEP (2.11). The optimal number of latent variables for the PLSR model under the SG.D1W11 pre-treatment was around 10, as indicated by the best.ncomp value of 9.30. The SG.D1W11 pre-treatment also had the same RMSEcv (1.93) and R^2cv (0.83) as the SG pre-treatment, suggesting that it also effectively reduced noise and enhanced the signal in the spectra data. The R^2sp for the SG.D1W11 pre-treatment was 0.78, indicating that it preserved the spectral information well.

The Raw data pre-treatment also showed a similar performance to the SG and SG.D1W11 pre-treatments, with identical values for RMSEp (2.10), R^2p (0.80), RPD (2.27), and RPIQ (2.80), and a slightly higher SEP (2.11). The optimal number of latent variables for the PLSR model under the Raw data pre-treatment was around 14, as indicated by the best.ncomp value of 13.70.

The Raw data pre-treatment also had the same RMSEcv (1.93) and R^2cv (0.83) as the SG and SG.D1W11 pre-treatments, suggesting that it did not affect the noise and signal in the spectra data. The R^2sp for the Raw data pre-treatment was 0.78, indicating that it preserved the spectral information well.

In contrast, the other pre-treatments demonstrated slightly inferior performance compared to the SG, SG.D1W11, and Raw data pre-treatments, with higher values for RMSEp, Bias, and SEP, and lower values for R^2p, RPD, RPIQ, CCC, and R^2cv. The SNV2D pre-treatment had the poorest performance among all the pre-treatments. It had the highest RMSEp (2.20), Bias (0.01), and SEP (2.20), and the lowest R^2p (0.78), RPD (2.17), RPIQ (2.68), CCC (0.88), and R^2cv (0.83). The optimal number of latent variables for the PLSR model under the SNV2D pre-treatment was around 13, as indicated by the best.ncomp value of 12.58. The SNV2D pre-treatment also had a higher RMSEcv (1.92) than the SG, SG.D1W11, and Raw data pre-treatments, suggesting that it increased the noise and decreased the signal in the spectra data. The R^2sp for the SNV2D pre-treatment was 0.77, indicating that it distorted the spectral information.

Contrary to the results obtained for starch prediction, the dry matter prediction results showed that the impact of pre-treatment methods on the model's performance was minimal, with negligible differences in statistical parameters among models using different pre-treatments. The best model was obtained with the D2 pre-treatment method, exhibiting slightly better performance in terms of RMSEp, R^2p, RPD, RPIQ, and CCC compared to other methods. This was in agreement with the findings of Maraphum *et al.* (2020) who reported the best results based on the spectra pre-treatment conducted through second derivative pre-treatment (D2). The authors reported a coefficient of determination of prediction set (R^2) and root mean square error of prediction (RMSEP) of 0.62 and 2.2, respectively. Conversely, the SGD1 pre-treatment method yielded the least favourable model, performing slightly worse than other methods in terms of bias and best.ncomp.

4.5 Conclusions

The values of R^2p obtained from this research viz: 0.62 and 0.8 for starch content and 0.7, 0.74 and 0.79 for dry mater content were similar to the prediction metrics that were reported in previous trials with respect to the consistency and accuracy of spectra (NIRS) data that were obtained using the SCiO sensor spectrometer. The results also affirmed that no single

pre-treatment algorithm has the unique inherent versatility to effectively handle noise from spectra data irrespective of other ancillary factors like, environmental conditions at the trial location, the uniqueness of the breeding population and the stage of breeding. This implies that care must be taken not to apply a blanket approach to every trial and accessions while selecting the appropriate pre-treatment algorithm to avoid model bias. This would be effectively taken care of through a holistic exploration of all the statistical metrics to choose the best pre-treatment algorithm. the same approach to everything without considering individual differences. Finally, the results showed that significant genetic gain could be achieved for both starch content and dry matter content in fresh cassava roots through selection.

CHAPTER FIVE

5.0 DEVELOPMENT OF HIGH THROUGHPUT PHENOTYPING PROTOCOL FOR EVALUATING YIELD AND PLANT ARCHITECTURE TRAITS IN CASSAVA, USING NORMALIZED DIFFERENCE VEGETATION INDEX (NDVI).

5.1 Introduction

Cassava (*Manihot esculenta* Crantz) is an important staple crop for global food security, particularly in the tropic and subtropical regions (Parmar *et al*., 2017; Tize *et al*., 2021). Due to climate change and population growth, there is a need to identify crops with potential for food security (EPA, 2016; Amelework *et al*., 2021; Dordley, 2022; IPCC, 2023). Cassava can benefit from climate change, making it a suitable candidate (Jarvis *et al*., 2012). Relentless efforts have been channelled into the development of improved cassava varieties, with several being released by the IITA and its partners (Hayes, 2020; BASICS-II, 2023). Continuous improvement is needed to ensure sustainable food production in this region. The highly heterozygous nature of the crop and the time required to raise seedlings from parents that are characterized with asynchronous flowering time make cassava improvement through conventional breeding more cumbersome (Maxmen, 2019). These factors also prolong the breeding cycle of cassava. Every process in the cassava breeding program is labour and capital intensive especially the harvesting and estimation of yield parameters and postharvest handling (Ceballos *et al*., 2020; Conceicão *et al*., 2023; Fei & Mahama, 2023).

The application of remote sensing technology could aid the rigour of harvesting, shorten the turnaround time of cassava breeding trials and reduce the cost of developing new varieties. A relationship could be established between cassava yield and the readings of the key plant architecture (morphological) traits measured at significant phenological stages of the crop (3, 6, 9 and 12) months after planting. This may lead to the development of accurate prediction models for phenotyping of large cassava trials (Tattaris *et al*., 2016; Machwitz *et al*., 2021; Marzougui *et al*., 2023). Normalized difference vegetation index (NDVI) is the most widely used of all the vegetation data for predicting crop yield (Huang *et al*., 2014; Panek & Gozdowski, 2020; Ji *et al*., 2021; Roznik *et al*., 2022). NDVI works based on the relationship between reflected and absorbed light in the red and near infrared bands.

$$\text{NDVI} = \frac{(NIR-Red)}{(NIR+Red)}$$

Where NIR- is the Near infrared band and Red – is the Red band.

Although the capital investment required to set up a remote sensing vegetative data collection platform for crop research in resource poor countries could be enormous and unaffordable, there is a possibility of achieving the collection of vegetative data (NDVI) with the aid of cheaper, and accurate handheld senor which could give precise data that could be used in developing a prediction model for cassava yield and other crop species (Kumhálová & Matějková, 2017; Zhang *et al*., 2019).

The Trimble GreenSeeker is one of these alternative technologies. The Trimble GreenSeeker is a handheld crop sensor that scans existing crops and provides a digitized NDVI reading. It uses red and infrared light to detect light reflection, indicating the strength of the light. The strength of the reflected light is measured and shown as a numeric reading between 0.00 and 0.99, based on the Normalized Difference Vegetation Index (NDVI). Higher values indicate healthier crops, while lower values indicate less healthy crops (Malveaux *et al*., 2015; Reynolds *et al*., 2015; Enciso *et al*., 2017; Jordan *et al*., 2019). The sensor is affordable, and user-friendly (Trimble, 2023).

The objective of this study was to develop an accurate and high-throughput phenotyping protocol for evaluating yield and plant architecture traits in cassava using Normalized Difference Vegetation Index (NDVI) data collected with the Trimble GreenSeeker.

5.2 Materials and Methods

5.2.1 Plant Materials

The collection of genotypes used for this trial comprised of 448 accessions that were selected from the clonal evaluation trial and five commercial varieties used as checks. The details of the accessions, including those of the crosses/parents used and the check varieties are shown in Table 3.1 of the appendices. The trial was conducted in two locations (Table 5.1) during the 2021/2022 planting season in Nigeria. The trial was laid out in a modified augmented block design with two replications per environment (location x season). Genotypes were assigned to incomplete blocks nested within replicates to control for field heterogeneity. The field layout contained both row and column coordinates, which allowed spatial modelling to account for possible field trends. Two to three commercial check varieties were included in

each block to provide benchmarks for performance comparison and quality control. A plot comprises three rows with three plants planted on ridges per row. A spacing of 1.0 m was maintained between ridges, while a spacing of 0.8 m was observed within plants in a row.

Table 5.1| The coordinates and weather data of the trial locations in Nigeria.

Location	GIS Coordinates	Altitude (MASL)	Average Rainfall (mm)	Average Temperature (°C)	Agroecological Zone
Onne	Lat 4.7363° N, Long 7.1545° E	6.8	2,700	26	Humid Forest
Mokwa	Lat 9.2934° N, Long 5.0493° E	180	1,200	32	Southern Guinea Savannah

MASL – Meters Above Sea Level, mm – Milimeters, °C – Degree Celcius

5.2.2 Phenotypic Data Collection

At specific phenological stages of the crop (3, 6, 9 and 12 months after planting), measurements were taken for the plant architecture and yield-related traits: The phenological stage and method used in measuring the traits in cassava were based on the guidelines outlined in Fukuda *et al*. (1998) and the NEXTGEN cassava trait ontology standard evaluation procedure contained in the (CassavaBase). The details of the trait evaluation are stated herein: Plant height was measured from the soil surface to the tip of the main stem at 3, 6, 9 and 12 months after planting (MAP). Height at the first branch was measured from the soil surface to the base of the first branch at 3, 6, 9 and 12 MAP. The angle of branching was measured as the angle between the main stem and the first branch at 9 MAP. Level of branching was measured as the number of branches per plant at 3, 6, 9 and 12 MAP. Branching habit was measured as the orientation of the branches (Erect, Dichotomous, Trichotomous and Tetrachotomous) at 9 MAP. Stem diameter was measured as the thickness of the main stem at 20 cm above the soil surface at 9 MAP. Dry matter content was measured at harvest (12 MAP) using the specific gravity method as described in Fukuda *et al*. (1998). The number of lodged plants per plot was counted and recorded; this entails plants that fell over or lodged at the base due to wind or pests at 9 MAP. Fresh root weight was measured as the total weight of fresh roots harvested per plot at harvest. Shoot weight was measured as the total weight of aboveground biomass (stems and leaves) per plot at harvest (12 MAP). Fresh root yield was calculated at harvest (12 MAP) by dividing the fresh root weight per plot by the highest number of stands harvested per plot and multiplied by 12,000 divided by 1000 which gives the value of the fresh root yield in tons per hectare. Top yield was calculated at harvest (12 MAP) by dividing the shoot weight per plot by the highest number of stands harvested per plot and multiplied by 12,000 divided by 1000 which gives the value of the top yield in tons per hectare. Dry yield was calculated at harvest (12 MAP) by dividing the value of fresh root yield by the value of the dry matter content multiplied by 100. The following traits: fresh root yield, dry yield, and top yield, were estimated in line with the protocol described by Hauser (2023) in the standard operating procedure for yield estimation in cassava. Harvest index was measured at harvest (12 MAP) as the ratio of fresh root weight to shoot weight per plot at harvest. The number of plants per stand was calculated at (9 MAP) as the number of plants that stemmed from each plant stand.

5.2.3 Collection of NDVI Data

5.2.4 NDVI Data Collection with a Trimble handheld sensor

The Trimble GreenSeeker (Figure 5.1), a vegetation sensor manufactured by the agricultural division of Trimble Inc USA, was used to capture the spectral properties of the cassava canopy. The sensor is made up of electroluminescent diodes (LEDs) that emit radiation in the red and near-infrared (NIR) regions. NDVI values were calculated based on the relationship between the red and near-infrared bands: (NIR-R)/(NIR+R), where NIR and R refer to the near-infrared and red reflectance, respectively (Farias *et al*., 2023). The normalized difference vegetation index (NDVI) values were measured using the Trimble GreenSeeker handheld NDVI meter device. The device emits red light at wavelengths within 660 nm, 25 nm FWHM (full width at half maximum), and near-infrared light at 780 nm and 25 nm FWHM. The device has two FOV (field of view) options: 25 cm at 60 cm: This means that when the device is positioned 60 cm away from the target, it captures an area with a width of 25 cm. 50 cm at 122 cm: Alternatively, when placed 122 cm away, it covers a wider area with a width of 50 cm. (Sahin, 2022).

The sensor was held at a height of 1 m above the canopy and pointed at a 45° angle towards the plants. The sensor was triggered at three points across the plants in the middle row within each plot, and the average NDVI value was recorded. The NDVI values can vary numerically from -1 to +1, with positive values indicating the vegetative vigour of the cassava plant, while negative values indicate the absence of vegetation or soil exposure. The data were collected at 3 months intervals, viz: 3, 6 and 9 months after planting. The plant height, height at first branch, and other plant architecture traits data were also collected at the same intervals, using the conventional methods.

Figure 5.1| Trimble GreenSeeker, a vegetation sensor

5.2.5 Data Analysis

5.2.6 Data Pre-processing:

The data was split into training (80%) and testing (20%) sets using the `createDataPartition` function from the `caret` package (Kuhn, 2019) of the (R Core Team, 2020). The seed was set to 123 for reproducibility. Reproducibility is crucial in data analysis, machine learning, simulations, and computational experiments to ensure reliability and validity. Whenever the seed is set to 123, it means that if the same code is run under the same conditions, the same results will be obtained. Any rows with missing values were removed.

5.2.7 Model Building and Calibration:

Two regression models (linear regression and polynomial regression model) were used for this analysis. A linear regression model (`lm`) was fitted with ground truth data of each of the yield and plant architecture traits used as the dependent variable and NDVI data obtained at 3, 6 and 9 months after planting used as the independent variable using the training data. This was done using the `lm` function from the `rms` package (Harrell, 2023) of the (R Core Team, 2020). The mathematical formula of the linear regression model is herein stated:

$FYLD = \beta_0 + \beta_1 * NDVI + \varepsilon$

FYLD – is the response variable, which is the fresh root yield

NDVI – is the predictor variable, which is the NDVI data taken at 3, 6 or 9 months after planting

β_0 – is the intercept term

β_1 – is the coefficient of the predictor variable NDVI

ε - is the error term

A polynomial regression model was developed to predict cassava fresh root yield (FYLD) based on several predictor variables. This was done using the `lm` function from the `leaps` package, version 3.1 (Miller, 2022) of the (R Core Team, 2020). The model included second-degree polynomial terms for each predictor variable to capture potential non-linear relationships. The predictors used in the model were: Normalized Difference Vegetation Index (NDVI), plant height (PLTHT), chlorophyll content (CHL), stem diameter (STMDI), angle of branching (ANGBR), number of lodged plants per plot (LODG), number of harvested plants per plot (NOHAV), and number of plants per stand (PPSTD). The mathematical formula of the polynomial regression model is herein stated:

$FYLD = \beta_0 + \beta_{11} * NDVI + \beta_{12} * NDVI^2 + \beta_{21} * PLTHT + \beta_{22} * PLTHT^2 + \beta_{31} * CHL + \beta_{32} * CHL^2 + \beta_{41} * STMDI + \beta_{42} * STMDI^2 + \beta_{51} * ANGBR + \beta_{52} * ANGBR^2 + \beta_{61} * LODG + \beta_{62} * LODG^2 + \beta_{71} * NOHAV + \beta_{72} * NOHAV^2 + \beta_{81} * PPSTD + \beta_{82} * PPSTD^2 + \varepsilon$

Each predictor variable X_ι (for $\iota = 1,2,\ldots,12$) is modelled with both its linear and quadratic terms to capture any non-linear relationships between the predictor variables and the response variable

Where:

FYLD – is the dependent variable, which is the fresh root yield

β_0 – is the model intercept term

$\beta_1(\iota = 1 \text{ to } n+1)$ – these are the model coefficients for each independent variable and its squared term. There are a total number of n+1 coefficients, where n is the number of independent variables (n=8)

ε - is the error term

NDVI – normalized difference vegetation index

PLTHT – plant height

CHL – chlorophyll content

STMDI – stem diameter

ANGBR – angle of branching

LODG – number of lodged plants per plot

NOHAV – number of harvested plants per plot

PPSTD – number of plants per stand

All these traits represent the independent variables used in developing the second-order polynomial regression model. For these three traits, normalized difference vegetation index, plant height, and chlorophyll content, measurements were taken at 3, 6 and 9 months after planting. Their corresponding values were used for the model development at these growth stages.

Model performance was evaluated using summary statistics and diagnostic plots generated by the `lm` function. The model was calibrated using bootstrapping with 100 iterations using the calibrate function from the `rms` package (Harrell, 2023) of the (R Core Team, 2020). The calibrate function in the `rms` package enhances resampling model calibration. It produces estimates of predicted versus observed values that have been corrected for bias or overfitting. The calibration results were printed and plotted using the print and plot functions.

5.2.8 Model Validation and Evaluation:

The calibrated model was used to predict the values of plant architecture and yield traits for the testing data set. This was done using the `predict` function from the `rms` package. Model performance was evaluated using the following statistical metrics:

R-squared (R^2) calculated using the `cor` function from the `base` package. It measures the proportion of variance in the plant architecture and yield traits explained by the NDVI predictor. Root Mean Squared Error (RMSE) calculated using basic mathematical operations. It quantifies the average deviation between predicted and observed values of plant architecture and yield traits. Mean Absolute Error (MAE) calculated using basic mathematical operations. It provides an average of the absolute errors between predicted and observed values of plant architecture and yield traits. Validation results were presented for R^2, RMSE, and MAE.

Analysis of variance of the plant architecture and yield traits was performed using the ` statgenGxE` package of the R software (R Core Team, 2020). The mathematical formula of the adopted model is herein stated:

The mathematical formular for the ANOVA model (linear mixed model)

$$Yijklm = \mu + Ei + R(E)\,j(i) + B(R\times E)\,k(ji) + Gl + (G\times E)il + \varepsilon ijklm$$

Where:

Yijklm: observed yield for the m-th plot in block k, replicate j, environment i, and genotype l

μ: overall mean

Ei: random effect of i-th environment assumed $N(0,\sigma^2E)$,

R(E)j(i): random effect of j-th replicate nested within the i-th environment $N(0,\sigma^2R)$,

B(R×E)k (ji): random effect of k-th block nested within replicate j and environment i $N(0,\sigma^2B)$,

Gl: fixed effect of l-th genotype,

(G×E)il : random effect of interaction between l-th genotype and i-th environment $N(0,\sigma^2GE)$,

εijklm: is random residual error, $N(0,\sigma^2\varepsilon)$.

The broad sense heritability (H^2) values were calculated as follows:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e^2}{er}}$$

Where H^2 is the broad sense heritability estimate, $\sigma^2 g$ is the genetic variance component of the accession effect, $\sigma^2 ge$ is the variance component of the genotype by environment effect, $\sigma^2 e$ is the variance component of the residual error, e is the number of environments and r is the number of replicates.

The estimation of genetic advance as a percentage of mean (GAM) was performed using the formula described in (Johnson *et al.*, 1955).

$$GAM = \frac{K \times \sigma p \times H}{100}$$

Where:

K = 2.06 at 5% selection intensity.

H = Heritability.

σp = Phenotypic standard deviation.

Genotypic and phenotypic correlation analysis for NDVI, plant architecture, and yield traits were performed using the statistical software Meta-R Version 6.0 (Alvarado *et al.*, 2020). Using the following model:

$y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \gamma_k + e_{ijk}$

y_{ijk} is the observation for the i-th genotype in the j-th block and the k-th replication

μ is the overall mean

α_i is the fixed effect of the i-th genotype

β_j is the random effect of the j-th block

$(\alpha\beta)_{ij}$ is the random interaction effect of the i-th genotype and the j-th block

γ_k is the random effect of the k-th replication within block

e_{ijk} is the residual error.

The estimates of the genetic and phenotypic correlations were obtained using the variance components from the linear mixed model:

$y = X\beta + Zu + e$

y is the vector of observations

β is the vector of fixed effects

u is the vector of random effects

e is the vector of residuals

X and Z are the design matrices.

The genetic correlation between two traits is calculated as:

$$rg = \frac{\sigma_{g1g2}}{\sqrt{\sigma^2_{g1}\sigma^2_{g2}}}$$

σ_{g1g2} is the covariance between the random effects of the two traits

σ^2_{g1} and σ^2_{g2} are the variances of the random effects of the two traits

The phenotypic correlation between two traits is calculated as:

$$rp = \frac{\sigma_{p1p2}}{\sqrt{\sigma^2_{p1}\sigma^2_{p2}}}$$

σ_{p1p2} is the covariance between the phenotypes of the two traits

σ^2_{p1} and σ^2_{p2} are the variances of the phenotypes of the two traits.

Data visualization was performed with the R package 'corrplot' version 0.92 (Wei & Simko, 2021).

Path Analysis was performed with the R package 'lavaan' version 0.6-17 (Rosseel, 2023).

Data visualization was performed with the R package 'semPlot' version 1.1.6 (Epskamp, 2022).

5.3 Results

The summary statistics of the NDVI data, plant architecture and yield traits for Mokwa trial (Table 5.2) and Onne trial (Table 5.3) showed that the accessions had differentially expressed performance for NDVI, plant architecture (angle of branching, stem diameter, shoot weight, number of lodged plants per plot, plant height at 3 months after planting, plant height at 6 months after planting, and plant height at 9 months after planting) and yield traits (root weight, dry matter content, starch content, fresh root yield, dry yield, top yield, and harvest index) in respect to each trial environments. Based on the mean values of these traits, higher values were reported from the trial conducted in Onne compared to that of Mokwa for all the traits except fresh root yield (FYLD) which was (24.08 t/ha) in Mokwa compared to (23.45 t/ha) in Onne, top yield (TYLD) 35.89 t/ha compared to 18.41 t/ha, NDVI at 3 months after planting 0.85 to 0.79, and plant height at 3 months after planting (PLTHT3) 110.58cm to 109.22cm. The error variance was lower than the genotypic variance for all the traits except for NDVI at 6 months after planting and levels of branching at 3 and 9 months after planting (Table 5.4). Broad sense heritability values ranged from 0.0 for NDVI data at 3 months after planting to 0.87 for height at the first branch at 3 months after planting. Moderately high values of broad sense heritability were recorded for important yield and quality traits like starch and dry matter content (0.61) as well as harvest index (0.66). The phenotypic coefficient of variation ranged from 0% for NDVI data at 3 months after planting to 69.88% for the number of lodged plants per plot, while genotypic coefficient of variation values ranged from 0% to 49.21% for these two traits respectively. The highest value of genetic advance as a percentage of the mean (71.57) was obtained for the number of lodged plants per plot while the least value of (0) was obtained for NDVI data at 3 months after planting. The analysis of variance (Table 5.5) for the NDVI, plant architecture (angle of branching, stem diameter, shoot weight, number of lodged plants per plot, plant height at 3 months after planting, plant height at 6 months after planting, and plant height at 9 months after planting) and yield traits (root weight, dry matter content, starch content, fresh root yield, dry yield, top yield, and harvest index) traits across the two environments showed that the accessions performed differently from one another for all the traits except for NDVI value at 6 months after planting.

Table 5.2| Summary statistics of the NDVI data, plant architecture and yield traits for the Mokwa trial

Trait	Min	Max	Mean	Variance	Coefficient of Variation
SHTWT	1.74	68.55	26.92	113.88	39.64
RTWT	0.55	46.25	18.06	70.1	46.36
DM	21.21	38.7	30.21	7.86	9.28
STARCH	3.93	27.23	15.92	13.93	23.44
FYLD	0.73	61.67	24.08	124.63	46.36
DYLD	0.97	18.61	7.63	11.22	43.9
TYLD	2.32	91.4	35.89	202.47	39.65
HI	0.05	0.81	0.4	0.01	25
NDVI3	0.37	0.92	0.85	0	5.26
NDVI6	0.24	0.8	0.6	0.01	14.91
NDVI9	0	0.79	0.61	0.01	13.72
LODG	0	9	1.35	2.75	122.84
PLTHT3	21	202.4	110.58	779.71	25.25
PLTHT6	52	231	130.44	802.12	21.71
PLTHT9	65	258	144.18	848.11	20.2
ANGBR	0	117.05	69.3	594.4	35.18
STMDI	9.82	33.14	21.47	10.67	15.21

SHTWT – shoot weight, RTWT – root weight, DM – dry matter content, STARCH – starch content, FYLD – fresh root yield, DYLD – dry yield, TYLD – top yield, HI – harvest index, NDVI3 – NDVI data at 3 months after planting, NDVI6 - NDVI data at 6 months after planting, NDVI9 - NDVI data at 9 months after planting, LODG – number of lodged plants per plot, PLTHT3 – plant height at 3 months after planting, PLTHT6 - plant height at 6 months after planting, PLTHT9 - plant height at 9 months after planting, ANGBR – angle of branching, and STMDI – stem diameter.

Table 5.3| Summary statistics of the NDVI data, plant architecture and yield traits for the Onne trial

Trait	Min	Max	Mean	Variance	Coefficient of Variation
SHTWT	1.02	66.2	18.41	93.76	52.6
RTWT	1.15	63.25	23.45	115.35	45.8
DM	25.1	43.75	33.62	8.16	8.5
STARCH	9.12	33.96	20.47	14.47	18.58
FYLD	1.15	63.25	23.45	115.35	45.79
DYLD	1.03	22.36	8.27	13.22	43.97
TYLD	1.02	66.2	18.41	93.73	52.59
HI	0.09	0.94	0.56	0.01	17.86
NDVI3	0.52	0.88	0.79	0.002	5.66
NDVI6	0.5	0.91	0.86	0.06	28.48
NDVI9	0.5	0.93	0.84	0.002	5.32
LODG	1	12	2.24	3.2	79.86
PLTHT3	48	186	109.22	385.7	40.92
PLTHT6	75	284	158.29	766.7	17.49
PLTHT9	106	366	203.71	1183.16	16.89
ANGBR	0	125.17	72.68	1295.6	49.52
STMDI	12.43	41.14	24.62	22.42	19.23

SHTWT – shoot weight, RTWT – root weight, DM – dry matter content, STARCH – starch content, FYLD – fresh root yield, DYLD – dry yield, TYLD – top yield, HI – harvest index, NDVI3 – NDVI data at 3 months after planting, NDVI6 - NDVI data at 6 months after planting, NDVI9 - NDVI data at 9 months after planting, LODG – number of lodged plants per plot, PLTHT3 – plant height at 3 months after planting, PLTHT6 - plant height at 6 months after planting, PLTHT9 - plant height at 9 months after planting, ANGBR – angle of branching, and STMDI – stem diameter.

Table 5.4| Estimates of variance components, broad sense heritability, PCV, GCV, and genetic advance for NDVI data, plant architecture and yield traits for all the cassava accessions evaluated across two environments in Nigeria.

Trait	Mean	σ^2g	σ^2_{GxE}	σ^2e	σ^2p	H^2	PCV(%)	GCV(%)	GA	GAM
DM	31.90	3.02	1.37	0.59	4.98	0.61	6.99	5.45	2.80	8.76
NOHAV	6.50	1.07	0.48	0.81	2.35	0.46	23.58	15.91	1.44	22.17
RTNO	48.00	130.37	46.82	73.05	250.24	0.52	32.96	23.79	17.02	35.46
SHTWT	22.65	26.28	9.50	15.06	50.84	0.52	31.48	22.63	7.61	33.60
RTWT	20.77	26.11	10.53	11.28	47.92	0.54	33.33	24.60	7.79	37.50
STARCH	18.20	5.36	2.42	1.05	8.83	0.61	16.32	12.72	3.73	20.47
FYLD	23.76	34.97	11.83	15.23	62.03	0.56	33.15	24.89	9.17	38.59
DYLD	7.95	2.62	1.46	1.66	5.74	0.46	30.12	20.36	2.26	28.42
TYLD	27.12	34.90	12.59	22.45	69.94	0.50	30.84	21.78	8.62	31.78
HI	0.48	0.0048	0.24	0.0012	0.2412	0.66	17.7	14.434	0.12	24.29
NDVI3	0.82	0.0002900	0.00	0.0018200	0.00	0.00	0.00	0.00	0.00	0.00
NDVI6	0.73	0.0000000	0.00	0.0100000	0.01	0.00	13.70	0.00	0.00	0.00
NDVI9	0.73	0.0000000	0.00	0.0000000	0.00	0.00	0.00	0.00	0.00	0.00
LODG	1.60	0.62	0.12	0.52	1.25	0.50	69.88	49.21	1.15	71.57
PLTH3	109.87	202.38	14.70	88.40	305.48	0.66	15.91	12.95	23.91	21.76
BRNHT3	55.85	304.95	3.71	41.48	350.14	0.87	33.50	31.27	33.65	60.26
BRNLEV3	1.60	0.01	0.04	0.05	0.09	0.11	18.75	6.25	0.07	4.30
PLTHT6	144.60	340.40	36.59	96.98	473.97	0.72	15.06	12.76	32.29	22.33
BRNHT6	68.10	95.33	206.51	41.31	343.15	0.28	27.20	14.34	10.63	15.60
BRNLEV6	2.00	0.13	0.09	0.05	0.27	0.49	25.74	18.03	0.52	26.07
PLTHT9	174.60	402.33	62.29	127.01	591.62	0.68	13.93	11.49	34.16	19.56
BRNHT9	85.10	473.15	102.22	60.97	636.34	0.74	29.64	25.56	38.73	45.51
BRNLEV9	2.50	0.02	0.12	0.04	0.18	0.11	16.73	5.66	0.10	3.95
CHL3	49.00	4.77	0.07	1.30	6.13	0.78	5.05	4.46	3.98	8.12
CHL6	47.89	3.02	0.51	1.28	4.81	0.63	4.58	3.63	2.84	5.94
CHL9	45.60	5.16	2.97	1.85	9.98	0.52	6.93	4.98	3.37	7.40
ANGBR	171.00	492.45	99.22	50.86	642.52	0.77	14.82	12.98	40.12	23.46
STMDI	23.10	6.34	1.42	2.02	9.78	0.65	13.54	10.90	4.19	18.13
PPSTD	2.00	0.10	0.02	0.08	0.20	0.51	22.22	15.81	0.46	23.23

STMDI - stem diameter, FYLD - fresh root yield, DYLD - dry yield, STARCH – starch content, DM – dry matter content, RTWT – fresh root weight, SHTWT – shoot weight, PLTHT9 – plant height at 9 months after planting, LODG – number of lodged plants per plot, HI – harvest index, ANGBR9 – angle of branching, RTNO – number of harvested roots, PPSTD9 – number of plants per stand, BRNHT9 – height at the first branch at 9 months after planting, PLTHT6 – plant height at 6 months after planting, TYLD – top yield, BRNHT6 – height at the first branch at 6 months after planting, NOHAV – number of harvested plants per plot, NDVI3 – NDVI at 3 months after planting, NDVI6 - NDVI at 6 months after planting, NDVI9 - NDVI at 9 months after planting, PLTHT3 – plant height at 3 months after planting, BRNHT3 – height at the first branch at 3 months after planting, BRNLEV3 – level of branching at 3 months after planting, BRNLEV6 – level of branching at 6 months after planting, BRNLEV9 – level of branching at 9 months after planting, CHL3 – chlorophyl content at 3 months after planting, CHL6 – chlorophyl content at 6 months after planting, CHL9 – chlorophyl content at 9 months after planting, σ^2g – genotypic variance, σ^2e – residual variance, σ^2p – phenotypic variance, H^2 - broad sense heritability, PCV, phenotypic coefficient of variation, GCV- genotypic coefficient of variation, GA - Genetic advance, GAM - genetic advance as a percentage of mean.

Table 5.5| Analysis of variance (ANOVA) of the NDVI data, plant architecture and yield traits across two environments

	NDVI3	NDVI6	NDVI9	HI	LODG	PLTHT3	PLTHT6	PLTHT9	ANGBR9	STMDI	TYLD	DYLD	FYLD	STARCH	DM	RTWT	SHTWT
ENV	1.72***	29.72***	23.14***	11.8***	23.14***	1573**	247743.74***	247743.74***	3137.82***	2819.71***	125111.94***	118.92***	192.25*	6572.41***	3706.58***	11576.81***	29827.92***
BLK(ENV*REP)	0.006***	0.07	0.006***	0.009***	0.006***	384.34*	518.46***	518.46***	259.01*	11.04***	117.07***	12.09***	117.15***	6.13***	3.46**	84.63***	79.10**
REP(ENV)	0.17***	0.05	0.05***	0.01	0.05***	15686.45***	20057.5***	20057.5***	316.12	195.71***	1563.36***	80.66***	659.64***	14.49**	8.19*	441.03***	890.61***
GEN	0.003***	0.01	0.005***	0.03***	0.005***	1121.88***	1672.35***	1672.35***	2312.22***	32.66***	275.73***	22.16***	247.44***	33.69***	19.0***	190.93***	199.92***
GEN * ENV	0.00	0.01	0.005***	0.009***	0.005***	393.4***	489.39***	489.39***	654.54***	12.12***	141.63***	11.95***	105.99***	13.67***	7.71***	85.0***	99.43***
Residuals	0.00	0.06	0.00	0.00	0.00	312.35	326.15	326.15	200.059	6.99	83.44	5.94	54.68	3.95	2.23	40.85	56.33

***, **, * significant at: 0.1%, 1% and 5% respectively

NDVI3 – NDVI at 3 months after planting, NDVI6 - NDVI at 6 months after planting, NDVI9 - NDVI at 9 months after planting, HI – harvest index, LODG – number of lodged plants per plot, PLTHT3 – plant height at 3 months after planting, PLTHT6 – plant height at 6 months after planting, PLTHT9 – plant height at 9 months after planting, ANGBR9 – angle of branching, STMDI - stem diameter, TYLD – top yield, DYLD - dry yield, FYLD - fresh root yield, STARCH – starch content, DM – dry matter content, RTWT – fresh root weight, SHTWT – shoot weight

The exploratory analysis revealed the interrelationships among the plant architecture and yield traits. Based on the Pearson correlation coefficient values (r), correlation coefficient plots were used to visualize and quantify these relationships.

Based on the output of the analysis of the data obtained from the trial conducted in Mokwa (Figure 5.2), the phenotypic correlation coefficient matrix revealed a positive and significant relationship between dry matter content and starch content ($r = 0.99$, $p < 0.001$), this is an indication that cassava accessions that have high dry matter content tend to be rich in cassava starch. Similar trends were observed between root weight and fresh root yield ($r = 0.99$, $p < 0.001$), shoot weight and top yield ($r = 0.99$, $p < 0.001$), fresh root yield and dry root yield ($r = 0.95$, $p < 0.001$), plant height at 3 months after planting and 6 months after planting ($r = 0.93$, $p < 0.001$), plant height at 3 months after planting and 9 months after planting ($r = 0.88$, $p < 0.001$), also between plant height at 6 months after planting and 9 months after planting ($r = 0.95$, $p < 0.001$).

However, a negative and significant relationship was observed between the number of lodged plants per plot and harvest index ($r = -0.50$, $p < 0.001$). These kind of relationships were observed between height at the first branch at 3 months after planting and level of branching at 3 months after planting ($r = -0.59$, $p < 0.001$), height at the first branch at 6 months after planting and level of branching at 6 months after planting ($r = -0.68$, $p < 0.001$), and height at the first branch at 9 months after planting and level of branching at 9 months after planting ($r = -0.70$, $p < 0.001$).

Unlike in the output of the phenotypic correlation coefficients, there was a stronger and significant negative relationship between harvest index and the number of lodged plants per plot ($r = -0.72$, $p < 0.001$) (Figure 5.3). In addition to this, moderate, significant negative relationships were observed between the number of lodged plants per plot and fresh root yield ($r = -0.56$, $p < 0.001$), root weight ($r = -0.56$, $p < 0.001$), and number of harvested roots per plot ($r = -0.50$, $p < 0.001$) respectively. This shows that the higher the number of lodged plants per plot, the lesser the values of the key yield traits such as fresh root yield, number of harvested roots per plot, root weight and harvest index. Also, there were high positive and significant relationships between the number of lodged plants per plot and plant height at 3 months after planting ($r = 0.75$, $p < 0.001$), plant height at 6 months after planting ($r = 0.87$, $p < 0.001$), and plant height at 9 months after planting ($r = 0.79$, $p < 0.001$). This shows that the taller the plant grows, the more it is prone to lodging.

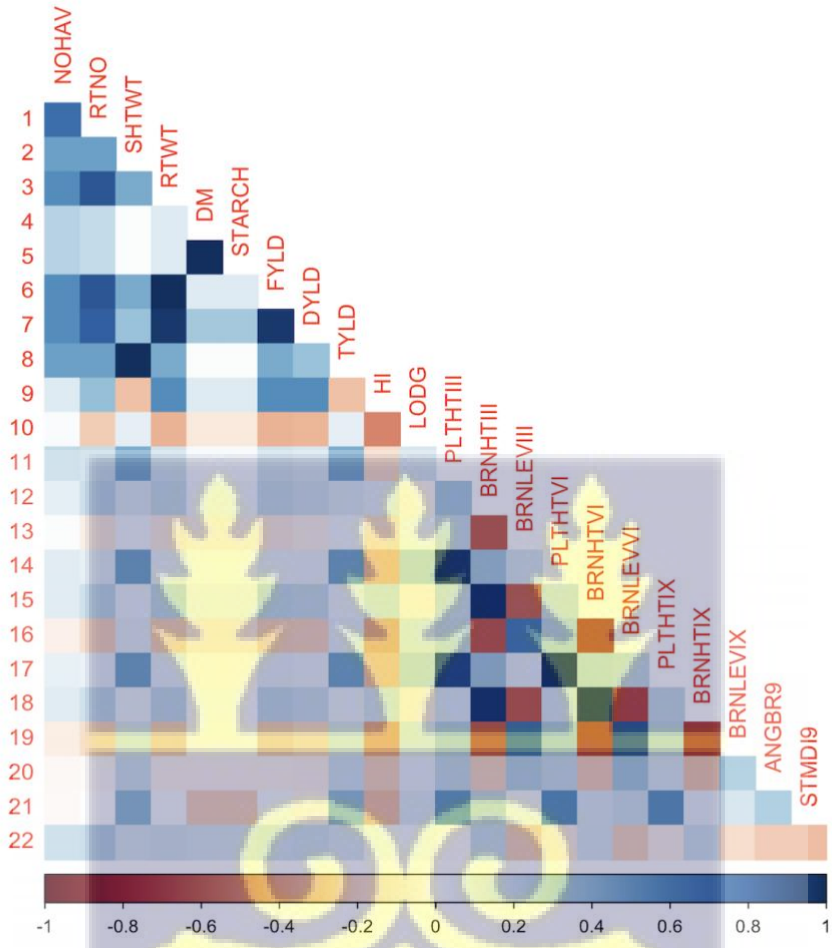

Figure 5.2| Phenotypic correlation coefficient plot of plant architecture and yield traits in the Mokwa trial

1 = NOHAV - number of harvested plants per plot, 2 = RTNO – number of harvested roots per plot, 3 = SHTWT – shoot weight, 4 - RTWT – root weight, 5 = DM – dry matter content, 6 = STARCH – starch content, 7 = FYLD – fresh root yield, 8 = DYLD – dry yield, 9 = TYLD – top yield, 10 = HI – harvest index, 11 = LODG – number of lodged plants per plot, 12 = PLTHTIII – plant height at 3 months after planting, 13 = BRNHTIII – height at the first branch at 3 months after planting, 14 = BRNLEVIII - level of branching at 3 months after planting, 15 = PLTHTVI – plant height at 6 months after planting, 16 = BRNHTVI – height at the first branch at 6 months after planting, 17 = BRNLEVVI - level of branching at 6 months after planting, 18 = PLTHTIX – plant height at 9 months after planting, 19 = BRNHTIX – height at the first branch at 9 months after planting, 20 = BRNLEVIX - level of branching at 9 months after planting, 21 = ANGBR9 – angle of branching, and 22 = STMDI9 – stem diameter.

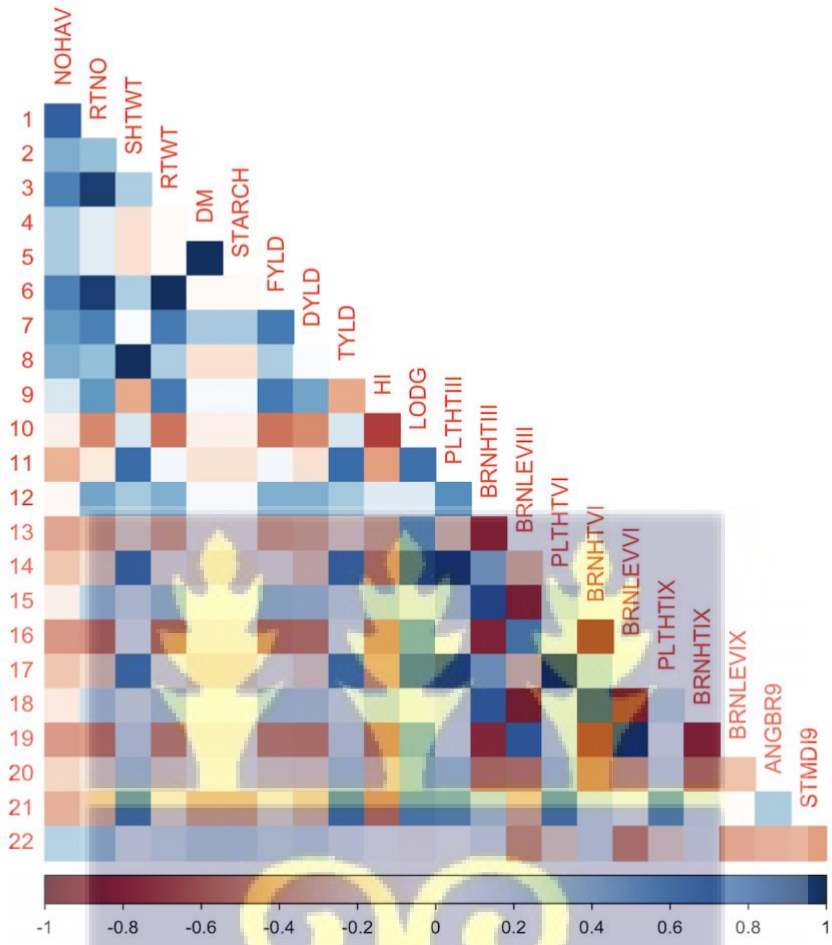

Figure 5.3| Genotypic correlation coefficient plot of plant architecture and yield traits in the Mokwa trial

1 = NOHAV - number of harvested plants per plot, 2 = RTNO – number of harvested roots per plot, 3 = SHTWT – shoot weight, 4 - RTWT – root weight, 5 = DM – dry matter content, 6 = STARCH – starch content, 7 = FYLD – fresh root yield, 8 = DYLD – dry yield, 9 = TYLD – top yield, 10 = HI – harvest index, 11 = LODG – number of lodged plants per plot, 12 = PLTHTIII – plant height at 3 months after planting, 13 = BRNHTIII – height at the first branch at 3 months after planting, 14 = BRNLEVIII - level of branching at 3 months after planting, 15 = PLTHTVI – plant height at 6 months after planting, 16 = BRNHTVI – height at the first branch at 6 months after planting, 17 = BRNLEVVI - level of branching at 6 months after planting, 18 = PLTHTIX – plant height at 9 months after planting, 19 = BRNHTIX – height at the first branch at 9 months after planting, 20 = BRNLEVIX - level of branching at 9 months after planting, 21 = ANGBR9 – angle of branching, and 22 = STMDI9 – stem diameter.

The output of the phenotypic correlation analysis for the yield traits in the Mokwa trial differs from the output obtained on the relationship between some plant architecture and yield traits in the trial conducted at Onne (Figure 5.4).

For instance, there were stronger negative, significant relationships between harvest index and shoot weight ($r = -0.52$, $p < 0.001$) and top yield ($r = -0.52$, $p < 0.001$) as well as compared to the ($r = -0.30$, $p < 0.001$) value obtained from these relationships on both trait in the Mokwa trial.

Likewise, the output of the genotypic correlation among yield and plant architecture traits in the Onne trial (Figure 5.5) showed weaker, negative, and significant relationships between the number of lodged plants per plot and harvest index ($r = -0.4$, $p < 0.001$) compared to the value ($r = -0.72$, $p < 0.001$) obtained in Mokwa trial. Contrary to the positive relationships recorded between number of lodged plants per plot and plant height in the Mokwa, low to moderate, plant height at 3 months after planting ($r = -0.1$, $p < 0.001$), and 9 months after planting ($r = -0.49$, $p < 0.001$) respectively were observed. Unlike in the Mokwa, this means that the taller plants in Onne grew, the lesser their propensity for lodging.

The path coefficient analysis revealed the direct and indirect contributions of the plant architecture traits to fresh root yield and root weight in cassava.

For the trial at Mokwa (Figure 5.6 & 5.7), root weight had an absolute (1.0) positive contribution to the fresh root yield. However, harvest index had a strong positive contribution to root weight (0.67), while the contributions of plant height at 9 months after planting (0.41) and 3 months after planting (0.17) were also positive. Contrary to these, negative relationships were observed for the number of lodged plants per plot (-0.12) and plant height at 6 months after planting (-0.18) with respect to their contributions to root weight.

Likewise, the root weight had absolute contributions to fresh root yield in the path coefficient analysis conducted on the data from the Onne trial (Figure 5.8 & 5.9). Plant height at 6 months after planting had strong positive contributions (1.06) to root weight while the reverse was the case for angle of branching with negative contribution (-0.30) and plant height at 6 months after planting (-0.21).

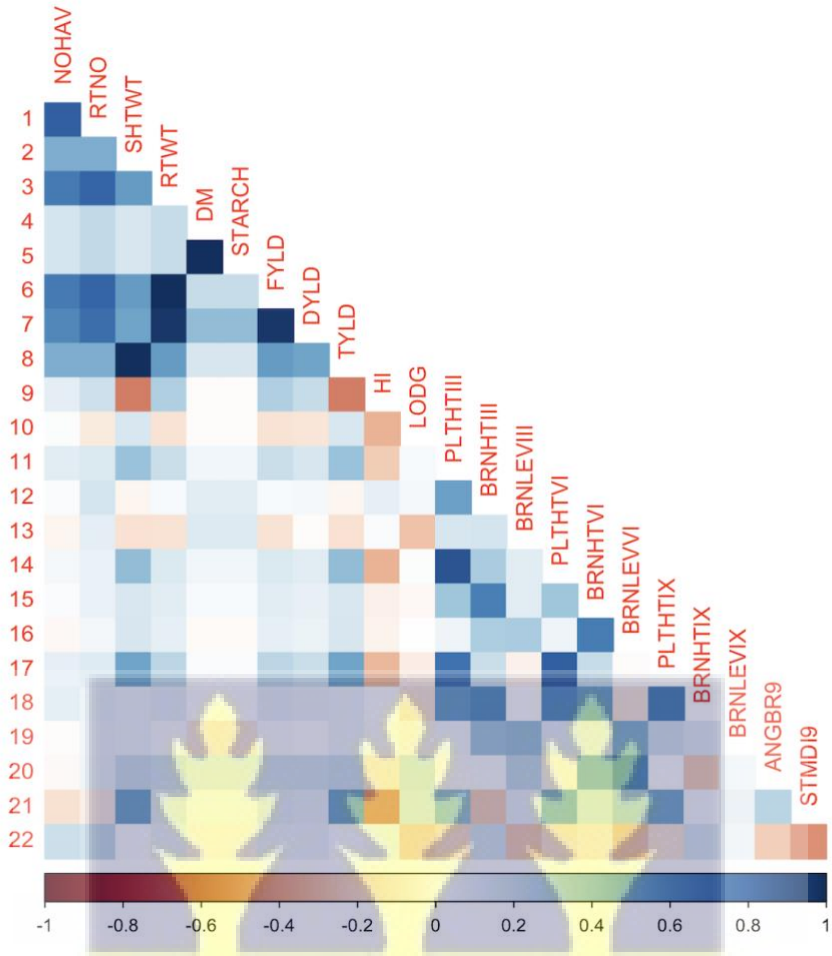

Figure 5.4| Phenotypic correlation coefficient plot of plant architecture and yield traits in the Onne trial

1 = NOHAV - number of harvested plants per plot, 2 = RTNO – number of harvested roots per plot, 3 = SHTWT – shoot weight, 4 - RTWT – root weight, 5 = DM – dry matter content, 6 = STARCH – starch content, 7 = FYLD – fresh root yield, 8 = DYLD – dry yield, 9 = TYLD – top yield, 10 = HI – harvest index, 11 = LODG – number of lodged plants per plot, 12 = PLTHTIII – plant height at 3 months after planting, 13 = BRNHTIII – height at the first branch at 3 months after planting, 14 = BRNLEVIII - level of branching at 3 months after planting, 15 = PLTHTVI – plant height at 6 months after planting, 16 = BRNHTVI – height at the first branch at 6 months after planting, 17 = BRNLEVVI - level of branching at 6 months after planting, 18 = PLTHTIX – plant height at 9 months after planting, 19 = BRNHTIX – height at the first branch at 9 months after planting, 20 = BRNLEVIX - level of branching at 9 months after planting, 21 = ANGBR9 – angle of branching, and 22 = STMDI9 – stem diameter.

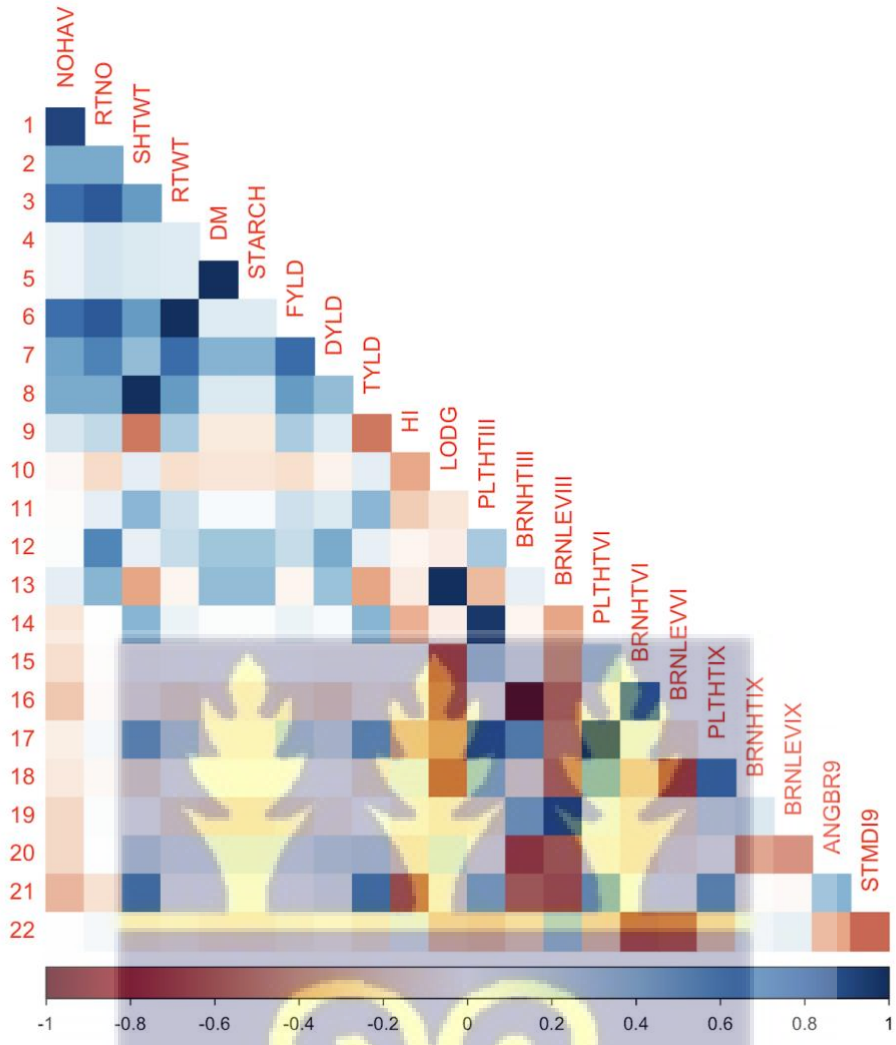

Figure 5.5| Genotypic correlation coefficient plot of plant architecture and yield traits in the Onne trial

1 = NOHAV - number of harvested plants per plot, 2 = RTNO – number of harvested roots per plot, 3 = SHTWT – shoot weight, 4 - RTWT – root weight, 5 = DM – dry matter content, 6 = STARCH – starch content, 7 = FYLD – fresh root yield, 8 = DYLD – dry yield, 9 = TYLD – top yield, 10 = HI – harvest index, 11 = LODG – number of lodged plants per plot, 12 = PLTHTIII – plant height at 3 months after planting, 13 = BRNHTIII – height at the first branch at 3 months after planting, 14 = BRNLEVIII - level of branching at 3 months after planting, 15 = PLTHTVI – plant height at 6 months after planting, 16 = BRNHTVI – height at the first branch at 6 months after planting, 17 = BRNLEVVI - level of branching at 6 months after planting, 18 = PLTHTIX – plant height at 9 months after planting, 19 = BRNHTIX – height at the first branch at 9 months after planting, 20 = BRNLEVIX - level of branching at 9 months after planting, 21 = ANGBR9 – angle of branching, and 22 = STMDI9 – stem diameter.

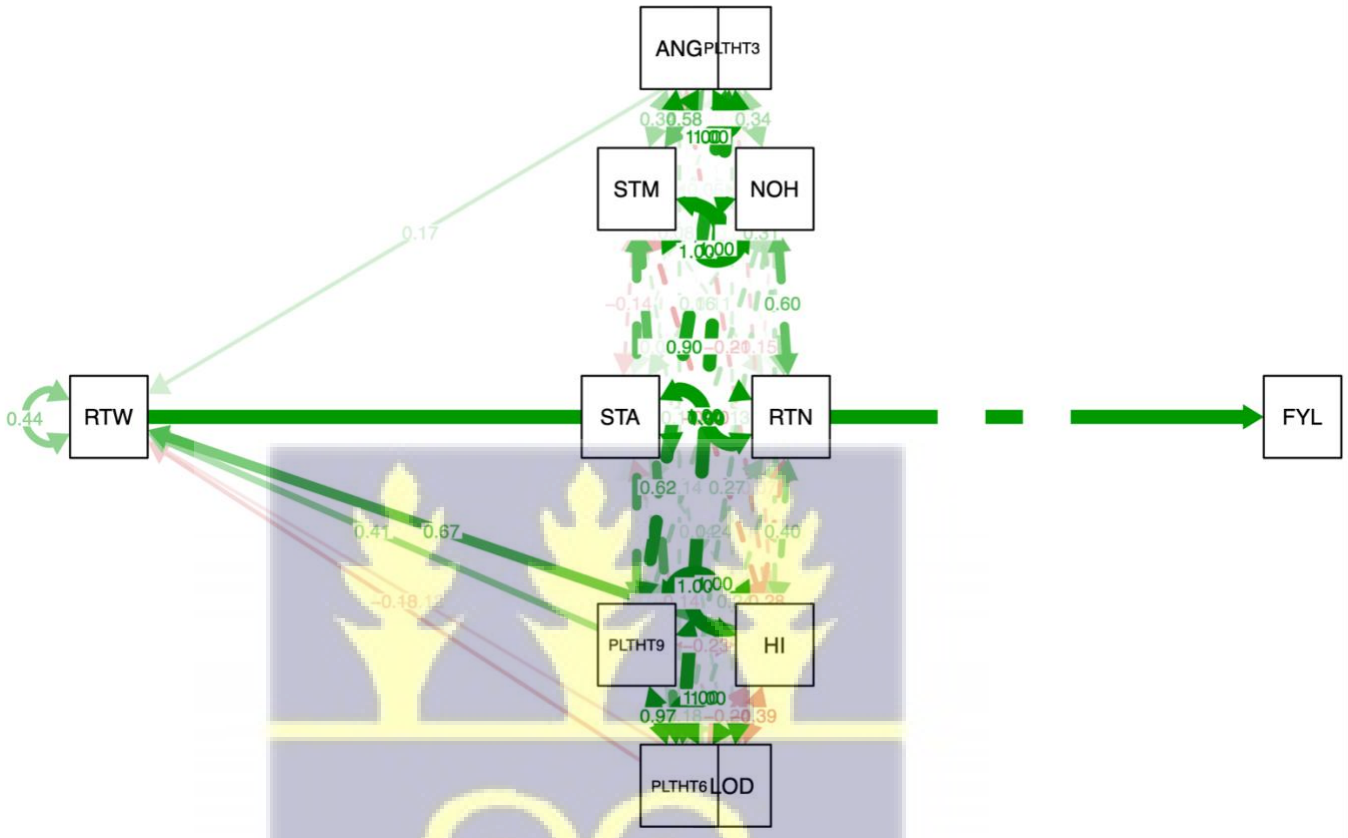

Figure 5.6| Path coefficient analysis plot of plant architecture and yield traits in the Mokwa trial

NOH - number of harvested plants per plot, RTN – number of harvested roots per plot, SHTWT – shoot weight, RTW – root weight, DM – dry matter content, STA – starch content, FYL – fresh root yield, HI – harvest index, LOD – number of lodged plants per plot, PLTHT3 – plant height at 3 months after planting, PLTHT6 – plant height at 6 months after planting, PLTHT9 – plant height at 9 months after planting, ANG – angle of branching, and STM – stem diameter.

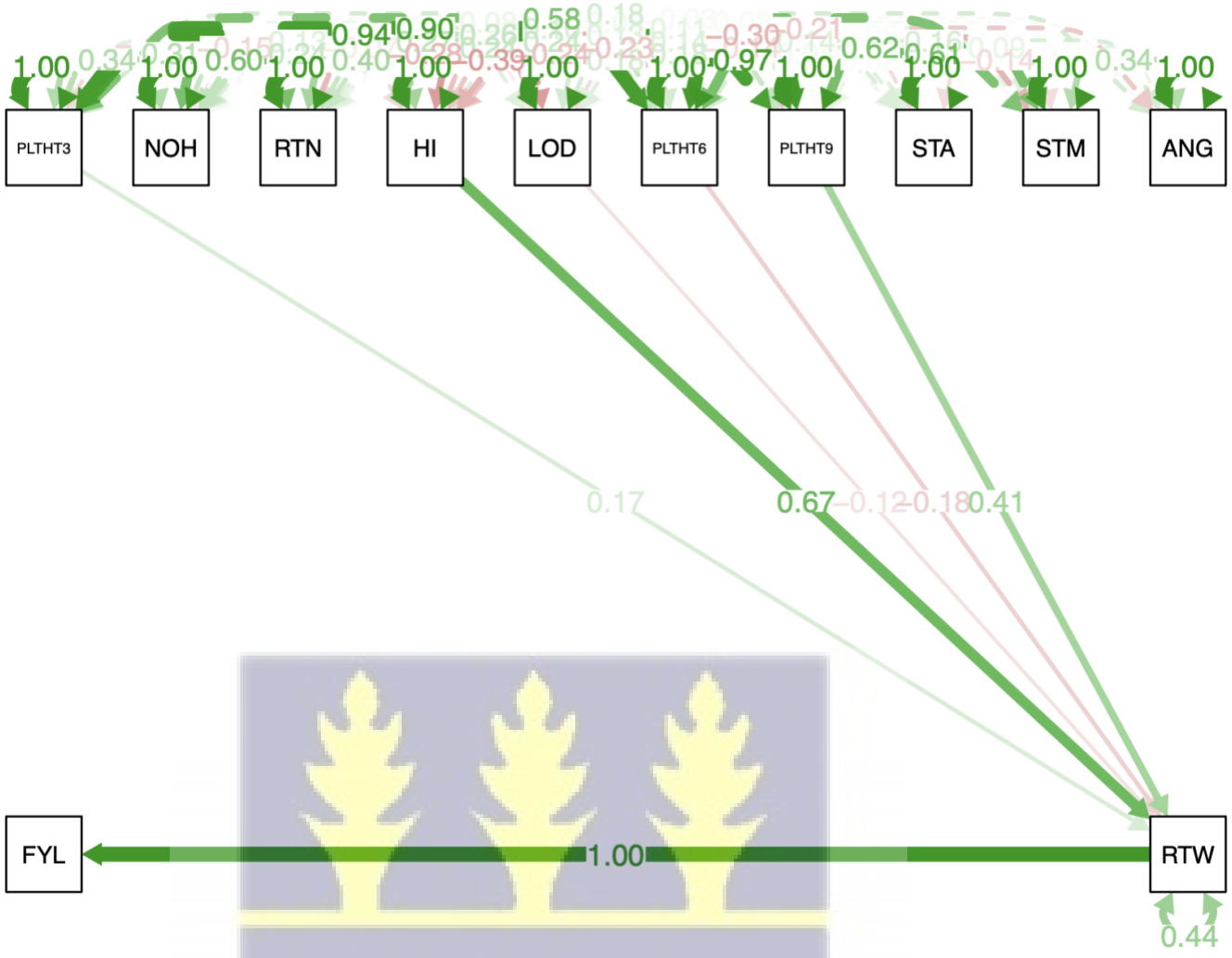

Figure 5.7| Path coefficient analysis plot of plant architecture and yield traits in the Mokwa trial

NOH - number of harvested plants per plot, RTN – number of harvested roots per plot, SHTWT – shoot weight, RTW – root weight, DM – dry matter content, STA – starch content, FYL – fresh root yield, HI – harvest index, LOD – number of lodged plants per plot, PLTHT3 – plant height at 3 months after planting, PLTHT6 – plant height at 6 months after planting, PLTHT9 – plant height at 9 months after planting, ANG – angle of branching, and STM – stem diameter.

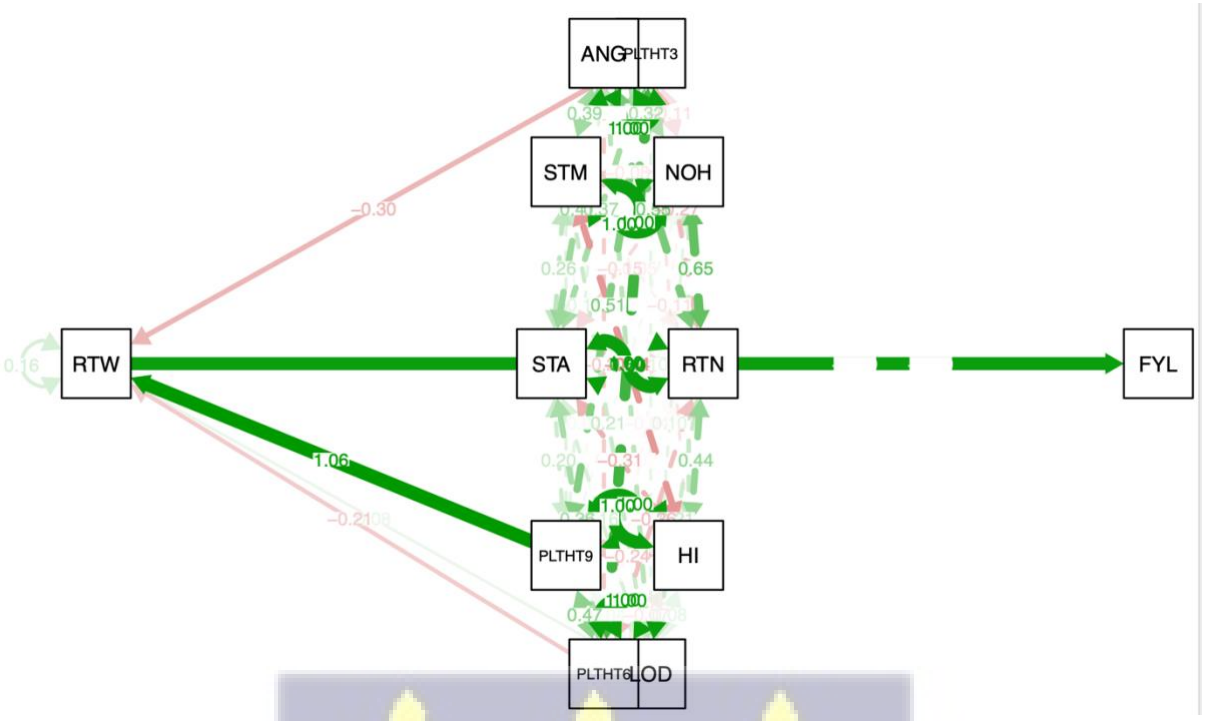

Figure 5.8| Path coefficient analysis plot of plant architecture and yield traits in the Onne trial

NOH - number of harvested plants per plot, RTN – number of harvested roots per plot, SHTWT – shoot weight, RTW – root weight, DM – dry matter content, STA – starch content, FYL – fresh root yield, HI – harvest index, LOD – number of lodged plants per plot, PLTHT3 – plant height at 3 months after planting, PLTHT6 – plant height at 6 months after planting, PLTHT9 – plant height at 9 months after planting, ANG – angle of branching, and STM – stem diameter.

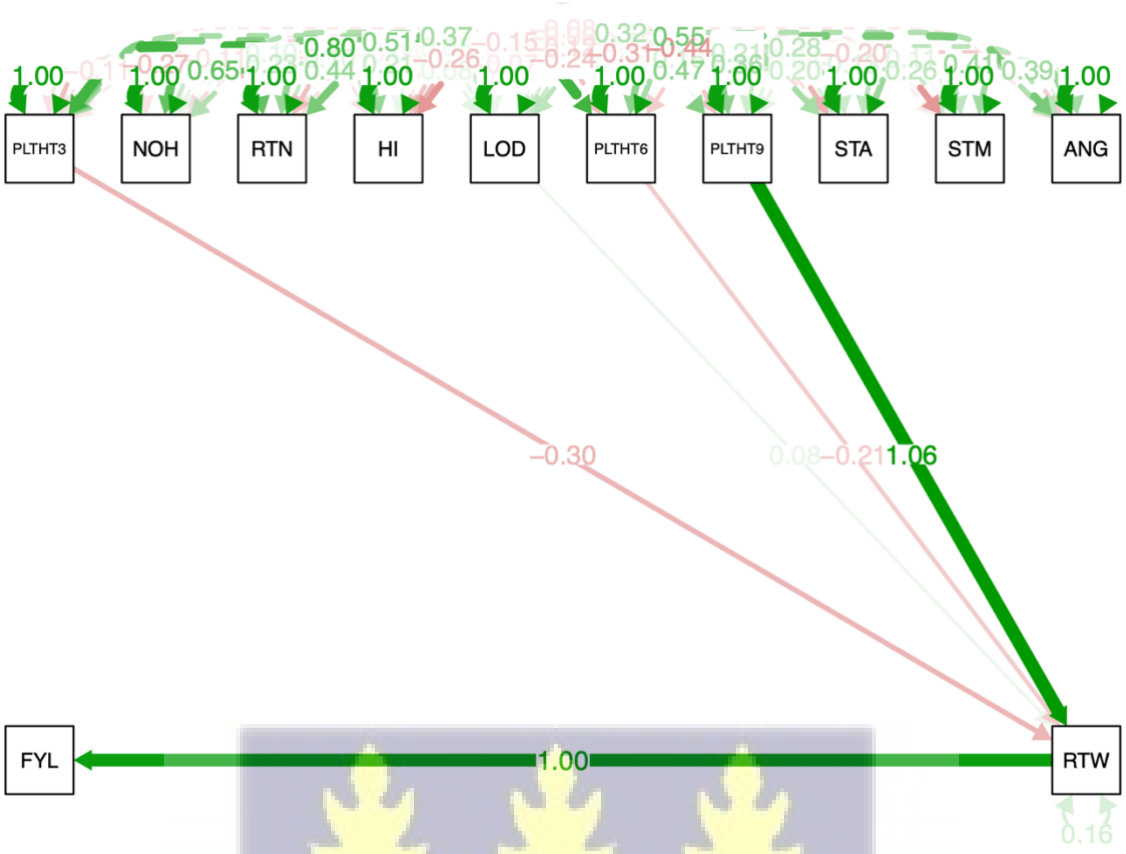

Figure 5.9| Path coefficient analysis plot of plant architecture and yield traits in the Onne trial

NOH - number of harvested plants per plot, RTN – number of harvested roots per plot, SHTWT – shoot weight, RTW – root weight, DM – dry matter content, STA – starch content, FYL – fresh root yield, HI – harvest index, LOD – number of lodged plants per plot, PLTHT3 – plant height at 3 months after planting, PLTHT6 – plant height at 6 months after planting, PLTHT9 – plant height at 9 months after planting, ANG – angle of branching, and STM – stem diameter.

The linear regression model prediction statistics (Table 5.6) for the prediction of plant architecture and yield traits using the NDVI data showed that the NDVI value at 3 MAP predicted the plant height at 3 MAP with high R^2 values (0.94) and NDVI value at 6 MAP for plant height at 6 MAP (0.7) respectively but with high root mean squared error (RMSE) values of 29.3 and 13.2 respectively, and mean absolute error (MAE) values of 27.3 and 11.7 respectively. Meanwhile, a high R^2 value of (0.9) was recorded for the prediction of fresh root yield, dry yield and root weight using the NDVI data collected at 6 months after planting, with relatively low values of RMSE (8.3, 2.2 and 6.2) respectively and MAE values of (7.4, 1.9 and 5.5) respectively for these traits. In the same vein, high R^2 value of (0.7) was recorded for harvest index for the prediction made using the NDVI data from 6 and 9 months after planting with very low RMSE values of (0.09 and 0.04) respectively and MAE values of (0.09 and 0.04) respectively. Similar result was reported from the prediction of stem diameter from the NDVI data obtained at 3 months after planting with R^2 value of (0.7) and relatively higher values of RMSE (1.9) and MAE (1.6).

Moderate values of R^2 (0.6, 0.4, 0.4 and 0.4) were recorded for dry yield and root weight both predicted from NDVI data at 9 moths after planting, starch content and dry matter content predicted from NDVI data at 3 months after planting, respectively. These traits also had relatively low values of RMSE (6.2, 4.7, 2.2 and 1.6) as well as MAE values of (4.5, 3.4, 1.8 and 1.3) respectively.

The prediction metrics obtained from the trial at Onne (Table 5.7) revealed lower R^2 values for the predicted traits compared to the values obtained from the Mokwa trial.

Moderate R^2 values of (0.5) were obtained on the prediction of fresh root yield, dry yield, and root weight, using the NDVI data collected at 9 months after planting. However, high values of RMSE (15.3, 5.3 and 15.3) were reported for these traits respectively as well as high values of MAE (13, 4.7 and 13).

However, a moderate R^2 value of (0.5) was reported for the prediction of harvest index, using the NDVI data collected at 3 months after planting with low RMSE value (0.1) and MAE value (0.07). Low R^2 values of (0.3, 0.3 and 0.4) were reported for starch content, dry matter content and stem diameter respectively from the NDVI data collected at 3 months after planting. Their RMSE values (3.8, 2.8 and 3.1) were relatively low as well as MAE values (3.1, 2.3 and 2.9).

The polynomial prediction statistics (Table 5.8) for the prediction of fresh root yield (FYLD) from the Normalized Difference Vegetation Index (NDVI), plant height (PLTHT), chlorophyll content (CHL), stem diameter (STMDI), angle of branching (ANGBR), number of lodged plants per plot (LODG), number of harvested plants per plot (NOHAV), and number of plants

per stand (PPSTD) showed the values of the model prediction statistics were quite similar across environment and the growth stage at which the data were collected. The R^2 value 0.39 was obtained for the data collected from the Mokwa trial at 3 and 6 months after planting and the Onne trial at 6 months after planting while R^2 value of 0.4 was recorded for the data collected from the Onne trial at 3 and 9 months after planting and the Mokwa trial at 9 months after planting. Similarly, MAE values of 6.3 was obtained for the data collected from Mokwa and Onne at 3 and 6 months after planting, with values of 6.2 and 6.4 for data obtained from Mokwa and Onne respectively at 9 months after planting. The RMSE values ranged from 7.8 to 8.2 for data obtained from Mokwa and Onne respectively at 9 months after planting.

Table 5.6| Linear regression model prediction statistics for plant architecture and yield traits from NDVI data at MOKWA for the 2021-2022 Trial

Trait	NDVI MOKWA 3MAP			NDVI MOKWA 6MAP			NDVI MOKWA 9MAP		
	R^2	RMSE	MAE	R^2	RMSE	MAE	R^2	RMSE	MAE
Plant Height	0.94	29.3	27.3	0.7	13.2	11.7	0.1	20.3	15
Fresh Root Yield	0.08	13.4	11.9	0.9	8.3	7.4	0.4	6.2	4.5
Dry Yield	0.1	4.1	3.5	0.9	2.2	1.9	0.6	1.4	1.1
Root Weight	0.07	10.1	8.9	0.9	6.2	5.5	0.4	4.7	3.4
Starch Content	0.4	2.2	1.8	0.2	1.5	1.2	0.3	2.2	1.4
Dry Matter Content	0.4	1.6	1.3	0.2	1.2	0.9	0.3	1.6	1
Shoot Weight	0.08	9.5	8.8	0.2	8.2	7.4	0	10.7	8.4
Harvest Index	0.01	0.1	0.1	0.7	0.09	0.09	0.7	0.04	0.04
Number of lodged plants per plot	0	0.7	0.6	0.1	0.9	0.9	0.2	0.9	0.7
Stem Diameter	0.7	1.9	1.6	0.4	3.1	3	0.2	3	2.3
Angle of Branching	0.3	6.5	5.6	0.1	6	5.2	0.2	7.3	6.1

R-squared (R^2), root mean squared error (RMSE), and mean absolute error (MAE)Months after planting (MAP).

Table 5.7| Linear regression model prediction statistics for plant architecture and yield traits from NDVI data at ONNE for the 2021-2022 Trial

Trait	NDVI ONNE 3MAP			NDVI ONNE 6MAP			NDVI ONNE 9MAP		
	R^2	RMSE	MAE	R^2	RMSE	MAE	R^2	RMSE	MAE
Plant Height	0.02	15.4	10.8	0.01	25	24.8	0.2	27.6	24
Fresh Root Yield	0.2	10.4	8.2	0.4	10.9	9.2	0.5	15.3	13
Dry Yield	0.2	3.8	2.9	0.3	4.2	3.4	0.5	5.3	4.7
Root Weight	0.2	10.4	8.2	0.4	11	9.2	0.5	15.3	13
Starch Content	0.3	3.8	3.1	0	3	2.7	0.2	3.9	2.5
Dry Matter Content	0.3	2.8	2.3	0	2.2	2	0.2	2.9	1.9
Shoot Weight	0.01	6.4	5.3	0.2	18.5	11	0.4	7.6	6.6
Harvest Index	0.5	0.1	0.07	0.01	0.07	0.04	0.3	0.09	0.1
Number of lodged plants per plot	0.1	1.5	1	0.04	1	0.8	0.2	1.4	1.1
Stem Diameter	0.4	3.1	2.9	0	2.1	1.9	0	2.8	2.8
Angle of Branching	0.04	35.7	31.5	0.1	50.5	48	0.2	42.2	40

R-squared (R^2), root mean squared error (RMSE), and mean absolute error (MAE)Months after planting (MAP).

Table 5.8| Polynomial regression model prediction statistics for fresh root yield at MOKWA & ONNE / 2021-2022 Trials

MOKWA

Trait	3MAP			6MAP			9MAP		
	R^2	RMSE	MAE	R^2	RMSE	MAE	R^2	RMSE	MAE
FYLD	0.39	7.9	6.3	0.39	7.9	6.3	0.4	7.8	6.2

ONNE

Trait	3MAP			6MAP			9MAP		
	R^2	RMSE	MAE	R^2	RMSE	MAE	R^2	RMSE	MAE
FYLD	0.4	8	6.3	0.39	8.1	6.3	0.4	8.2	6.4

5.4 Discussion

The cassava accessions were planted out in two distinct environments: the humid forest zone and the southern Guinea Savannah zone (Table 5.2). There was a strong genotype-by-environment interaction (GEI) for all the plant architecture and yield traits at ($p < 0.001$) except for the number of lodged plants per plot and plant height at 3 months after planting at ($p < 0.01$). This agreed with the findings of Bakare *et al*. (2022) who reported the presence of a strong interaction between cassava genotypes and test environments with respect to fresh root yield, dry yield, top yield, harvest index and dry matter content. Bakare *et al*. (2022) planted in five agroecological zones in Nigeria which included both the humid forest and the southern Guinea Savannah zone. Similar results were reported by Amelework *et al*. (2022) on trials conducted in three distinct locations that encompass both tropical and subtropical agro-ecological zones in South Africa. Amelework *et al*. (2022) observed significant variation among the test environments, genotype, and genotype-by-environment among the cassava accessions in respect to number of roots, root weight, fresh root yield, dry matter content, plant height, shoot weight and harvest index. In another trial, Ogwuche *et al*. (2023) reported similar results for the following traits; root number, fresh root yield, dry yield, dry matter content at ($p < 0.01$). Ogwuche *et al*. (2023) conducted their trials in eight locations in Nigeria that cut across four agroecological zones in which both the humid forest and the southern Guinea Savannah zones were represented.

The presence of genotype-by-environment interaction (GEI) for plant architecture and yield traits makes it difficult for cassava breeders to adequately select superior cassava genotypes for advancement in breeding programs. With the presence of GEI, effective selection of genotypes is rarely achieved due to disparity in the rankings of genotypes across different environments and introduction of bias that diminishes selection gains (Begna, 2022; Sampaio Filho et al., 2023).

Rattanasopa *et al*. (2022) used normalized difference vegetation index (NDVI), simple ratio vegetation index (RVI), and chlorophyll vegetation index (CIRedEdge) to predict the fresh root yield and height of cassava plants. The authors found out NDVI with R^2 value of 0.58 for fresh root yield and R^2 value of 0.87 for plant height produced the best prediction accuracy for fresh root yield. This 0.58 R^2 value was quite low, compared to the 0.9 R^2 value for the prediction of fresh root yield recorded at the trial in Mokwa using NDVI data collected at 6 months after planting. However, it was close to 0.5 R^2 value from the data collected at

Onne trial at 9 months after planting. Unlike the R^2 value obtained for yield prediction, the plant height values were closer to both values obtained from the data collected at Mokwa trial which were 0.94 and 0.7 for plant height at 3 and 6 months after planting respectively. Although, the models have high RMSE and MAE values which require revalidation on a new set of accessions and trials. In a similar study conducted by Ayu Purnamasari *et al.* (2019), on the use of vegetation indices data such as Normalized Difference Vegetation Index (NDVI), Soil Adjusted Vegetation Index (SAVI) and Infrared Emission Chlorophyll Index (IRECI) in predicting cassava yield, the authors reported that NDVI had the highest accuracy for cassava yield prediction with R^2 value of 0.62.

According to Grados & Schrevens (2020), the NDVI values taken from the cassava fields between 2 – 10 months after planting ranged between 0.3 – 0.4. These values were quite low compared to the lowest mean value of 0.60 recorded at 6 months after planting on the trial in Mokwa, and 0.79 at 3 months after planting recorded on the trial in Onne.

In the same vein the prediction accuracy of starch content and dry matter content using the NDVI data collected from Mokwa has the R^2 value of 0.4, though a little below average (0.5). The model is characterized by very low values of RMSE which ranged from 1.6 – 2.2 and RAE values which ranged from 1.3 – 1.8. These give much credence to the reliability of this model. This makes it possible to have a fair estimate of these important traits right from the field and allows for on-the-spot assessment and initial selection.

According to the research conducted by León *et al.* (2021), a mean value of dry matter content as low as 27.9 was reported with the highest mean value of 41. However, in the trial conducted at Mokwa and Onne, mean values of 30.21 and 33.62 were recorded respectively. This is an indication that the accessions have the inherent potential for exploration of genetic gains for dry matter content. Dry matter content is not only an important determinant of yield in cassava, but also highly correlated with starch content (Peprah *et al.*, 2020; Silva *et al.*, 2023; Malai *et al.*, 2024), which is an important indicator for cassava varieties that are suitable for industrial use. This was confirmed with the genetic correlation coefficient value of 0.99. By implication, effective selection for starch content could be carried out using the dry matter content. Given this moderately high estimate of broad sense heritability (0.61), for starch and dry matter content, there is significant potential for genetic improvement of these traits in cassava through selection. Johnson *et al.* (1955) grouped GAM into 3 categories as follows: GAM values that were less than 10% were low, values between 10-20% were classified as moderate while values that were more than 20% were high. The moderately high value of broad sense heritability (0.61) recorded for these traits and moderate genetic advance as a percentage

of mean (GAM) value of 20% for starch content indicate that the trait would respond favourably to selection, thereby resulting into enhanced improvement.

For example, selection for starch content, which has a heritability of 0.61 and genetic advance as a percentage of mean (GAM) value of 20% implies that imposing selection pressure on the top 5% of the base population could result in significant gains of 20% in starch content over time. This will enhance the improvement of the quality of cassava roots for industrial processing and consumption.

Plant height and stem diameter are also important plant architecture traits. Impressive prediction accuracy was obtained for these traits with plant height at 3 months after planting using the NDVI data collected in Mokwa at 3 months after planting with an R^2 value of (0.94) but relatively high values of RMSE (29.3) and MAE (27.3) and R^2 (0.7), RMSE (13.2) and MAE (11.7) for NDVI data collected at 6 months after planting in Mokwa trial. For stem diameter, using the NDVI data collected at 3 months after planting, a high R^2 value of (0.7) with very low RMSE (1.9) and low MAE (1.6) were realized; this suggests that this model is highly reliable for the estimation of this trait and it will facilitate rapid on-field assessment of this trait for real-time decision making.

Amarullah (2021), reported high values of 277.78 cm for plant height and 30 cm for stem diameter. However, in this trial, mean values of plant height ranged between 110.58cm to 203.71cm while the stem diameter ranged from 21.47 cm to 24.62 cm. There exist a positive and significant genotypic relationship between plant height and stem diameter. These traits were also positively correlated to the number of lodged plants per plot. However, all the three traits were negatively and significantly correlated with an important yield indicator, which is harvest index. This necessitates the need to strike a balance between these traits for enhanced productivity. With the high values of broad sense heritability reported for plant height, 0.68 – 0.72, and stem diameter, 0.65 it is possible to manipulate these traits to develop plants with ideal architecture and improved yield.

The genotypic correlation coefficients showed that traits like root dry yield, root weight, harvest index and number of roots were positively and significantly correlated with the principal yield determinant, fresh root yield. This is in agreement with the findings of Edet *et al*. (2015). This was also confirmed in the output of the path coefficient analysis which showed that root weight had an absolute contribution to the fresh root yield. Meanwhile, traits like harvest index, plant height at 3 and 9 months after planting had positive contributions to fresh root yield through the root weight while number of lodged plants per plot and plant height at 6 months after planting made negative contributions to the fresh root yield through the root

weight. Edet *et al*. (2015), also observed a negative relationship between plant height and fresh root yield at 1 month after planting.

Mehari *et al*. (2015) ranked broad sense heritability as follows: low ($h^2 < 0.30$), moderate ($0.30 \leq h^2 \leq 0.60$) and high ($h^2 > 0.60$). Based on these classifications, broad sense heritability for both plant architecture and yield traits in this study across environments ranged from low to high: NDVI at 3 and 9 months after planting (0.0), levels of branching at 3 and 9 months after planting (0.11), stem diameter (0.65), fresh root yield (0.56), root weight (0.54), plant height at 9 months after planting (0.68), harvest index (0.66), starch content (0.61), dry matter content (0.61) and angle of branching (0.77). Similar results were reported by Ewa *et al*. (2017) on dry matter content (0.47) and fresh root yield (0.25). The range of the broad sense heritability values reported in this study are also consistent with the findings of Peprah et al. (2020), who reported broad sense heritability value of (0.41) for number of harvested roots, as well as Adu *et al*. (2020b) who reported harvest index value of (0.58), and fresh root weight (0.45). Harvest index (HI) is a measure of the efficiency of a crop in converting assimilated photosynthate (source) into economic yield (sink) (Alemu, 2021). The presence of moderately high values of broad sense heritability for harvest index 0.49 and high genetic advance as a percentage of mean (GAM) value of 21% shows that there is huge potential for desirable response to selection and optimization of cassava plants for this trait through recombination of favourable alleles.

However, broad sense heritability for NDVI data ranged from (0.008) to (0.13), so this shows that the environmental component of the phenotypic variance had a larger impact on the values of the NDVI data and this could explain the disparity observed in the degree of accuracy of the linear regression models developed using the data from the two trial environments.

5.5 Conclusions

In this research, two separate models (linear regression model and polynomial regression model) were used in developing phenotyping protocols that could be used in predicting the values of yield and plant architecture traits in cassava, using the Normalized Difference Vegetation Index (NDVI) data collected with the handheld Trimble GreenSeeker.

The results that were obtained using the polynomial regression model to predict fresh root yield from a number of variables which include: NDVI data, plant height, chlorophyll content, stem diameter, angle of branching, number of lodged plants per plot, number of harvested plants per plot, and number of plants per stand showed that the prediction accuracy for the fresh root yield

across the two environments were more or less the same at 3, 6 and 9 months after planting. However, the values of (R^2) that signify the reliability of the prediction models were quite low.

Unlike the polynomial regression model where several variables were used in predicting the fresh root yield, the linear regression model entails the use of NDVI data in predicting the yield or the plant architecture trait directly and one trait at a time. Based on the results obtained from the prediction models that were developed using the linear regression model, there exist huge disparity between the data obtained from Mokwa and Onne trials with respect to the accuracy of prediction of the yield and plant architecture traits. Generally, higher coefficient of determination (R^2) values, which signify more reliable prediction accuracy and lower values of root mean squared error (RMSE) and mean absolute error (MAE) were observed for the plant architecture and yield traits using the NDVI data collected from Mokwa compared to that of Onne. This suggests that the disparity in prevailing environmental conditions could influence the accuracy of model development. This implies that the findings of this experiment should be subjected to further validation on a new set of cassava accessions and in different environments.

CHAPTER SIX

6.0 GENOTYPE BY ENVIRONMENT INTERACTION AND STABILITY ANALYSIS OF CASSAVA GENOTYPES FOR YIELD AND PLANT ARCHITECTURE TRAITS.

6.1 Introduction

Cassava (*Manihot esculenta* Crantz) ranks as the fourth most important staple crop and a significant source of calories in the tropics, after wheat, rice and maize (FAO, 2020b). Cassava is being cultivated and consumed by more than 500 million people in more than 25 countries across the globe (Cook, 2023). Fresh cassava roots is a rich source of carbohydrate, it can produce up to 191 calories per 100 gram of cooked fresh cassava roots (Chin *et al*., 2023). In addition to this, fresh cassava roots can be processed into valuable products such as flour, starch, ethanol and animal feeds (DOING, 2019). Cassava is valued for its high yield potential and ability to produce food and income for resource-poor farmers as well as forex earnings for farmers who cultivate the crop on a commercial scale. The crop has an average global yield of about. 10.5 tons per hectare but could be as high as 14.5 tons per hectare in Thailand (FAOSTAT, 2021).

However, cassava production and yield are being limited by a complex of biotic and abiotic factors which include: pests and diseases, low soil fertility, coupled with the overall effects of changing climate (Devi *et al*., 2022).

Cassava breeders have developed and released several suitable cassava varieties through the long-term collaborative research among organizations like, National Root Crops Research Institute (NRCRI) and the International Institute of Tropical Agriculture (IITA) in Nigeria. The improved cassava varieties were developed to address the factors that impose constraints on cassava production and maximization of its yield potential (Bakum, 2020). However, considering the erratic nature of the factors limiting cassava production, there is need for continuous improvement of cassava and release of suitable varieties that can adapt to the dynamic agroecosystem with utmost satisfaction of end-users' needs.

Plant architecture is an important trait for cassava improvement for adaptability, fresh root yield and suitability for mechanized cultivation (Mora Moreno *et al*., 2016; Adu *et al*., 2018; Srisawad *et al*., 2022).

Another important trait for cassava improvement is fresh root yield, which is the quantity of edible roots produced per unit area. Yield and yield-related traits constitute the goal of cassava breeding. These are the determinants of the economic value and food security

potential of the crop (Braatz de Andrade *et al*., 2022; Fei, 2016; Ojulong *et al*., 2010). Yield is a complex trait that is influenced by many factors, such as genotype, environment, and genotype by environment interaction (Bakare *et al*., 2022; Uchendu *et al*., 2022).

Cassava exhibits a high degree of genotype by environment interaction (GEI) for yield and yield related traits (Bakare *et al*., 2022; Uchendu *et al*., 2022). This implies that genotypes express significant differential in their performance in respect to the prevailing environmental conditions. This implies that cassava breeders must evaluate a large number of genotypes across multiple environments to identify superior and stable genotypes that can adapt to diverse and dynamic agroecosystems. Ojulong *et al*. (2010) recommended the adoption of crucial selection indices at the early stage of breeding to shorten the breeding cycle in cassava. The indices highlighted by Ojulong *et al*. (2010) include fresh root yield, percentage dry matter content, root weight, harvest index and roots per plant.

Effective application of selection index for the genetic improvement of these key traits in cassava is a function of the level of understanding of the genetic variability, heritability, and genetic advance of these traits (Falconer & Mackay, 2009; Allard, 1999). Genotype by environment interaction (GEI) is a significant phenomenon affecting trait expression across different environments. Comprehending GEI is crucial for identifying genotypes with stable performance across diverse environments (Falconer & Mackay, 2009).

The objectives of this study were to:

1. evaluate the effect of genotype by environment interaction on plant architecture and yield traits among the cassava accessions used for this trial across five environments, and
2. identify best performing and stable cassava accessions for fresh root yield and starch content among the cassava accessions used for this trial across five environments.

6.2 Materials and Methods

6.2.1 Plant Materials

The cassava accessions used for this research were developed by the cassava breeding unit of the International Institute of Tropical Agriculture (IITA), Ibadan. The accessions used were obtained from the clonal evaluation trial of the breeding program. The collection of genotypes used for this trial comprised 453 cassava accessions, including 448 accessions that were selected from the clonal evaluation trial and five commercial varieties used as checks. The details of the accessions, including those of the crosses/parents used and the commercial check varieties are shown in (Table 3.1) of the appendices. The trial was conducted in five environments (a combination of specific planting season and location makes one environment) across four locations (Table 6.1) and across four planting seasons (2019/2020, 2020/2021, 2021/2022, and 2022/2023) in Nigeria. The trial was laid out in a modified augmented block design with two replications per environment (location x season). Genotypes were assigned to incomplete blocks nested within replicates to control for field heterogeneity. The field layout contained both row and column coordinates, which allowed spatial modelling to account for possible field trends. Two to three commercial check varieties were included in each block to provide benchmarks for performance comparison and quality control. A plot comprises three rows with three plants planted on ridges per row. A spacing of 1.0 m was maintained between ridges, while a spacing of 0.8 m was observed within plants in a row.

Table 6.1| The coordinates and weather data for the trial locations in Nigeria

Location	GIS Coordinates	Altitude (MASL)	Average Rainfall (mm)	Average Temperature (°C)	Agroecological Zone
Ikenne	Lat 6.8718° N, Long 3.7106° E	90	2,000	27	Humid Forest
Onne	Lat 4.7363° N, Long 7.1545° E	6.8	2,700	26	Humid Forest
Mokwa	Lat 9.2934° N, Long 5.0493° E	180	1,200	32	Southern Guinea Savannah
Kano	Lat 12.0022° N, Long 8.5917° E	470	1,000	35	Semi Arid/Sudan Savannah

MASL – Meters Above Sea Level, mm – Milimeters, °C – Degree Celcius

6.2.2 Phenotypic Data Collection

At specific phenological stages of the crop (9 and 12 months after planting), measurements were taken for the plant architecture and yield-related traits: The phenological stage and method used in measuring the traits in cassava were based on the guidelines outlined in Fukuda *et al*. (1998) and the NEXTGEN cassava trait ontology standard evaluation procedure contained in the (CassavaBase).

Plant height was measured from the soil surface to the tip of the main stem at 9 months after planting (MAP). The angle of branching was measured as the angle between the main stem and the first branch at 9 MAP. Branching habit was measured as the orientation of the branches (Erect, Dichotomous, Trichotomous and Tetrachotomous) at 9 MAP. Stem diameter was measured as the thickness of the main stem at 20 cm above the soil surface at 9 MAP. Dry matter content was measured at harvest (12 MAP) using the specific gravity method as described in Fukuda *et al*. (1998). The number of lodged plants per plot was counted and recorded; this entails plants that fell over or lodged at the base due to wind or pests at 9 MAP. Fresh root weight was measured as the total weight of fresh roots harvested per plot at harvest. Shoot weight was measured as the total weight of aboveground biomass (stems and leaves) per plot at harvest (12 MAP). Fresh root yield was calculated at harvest (12 MAP) by dividing the fresh root weight per plot by the highest number of stands harvested per plot and multiplied by 12,000 divided by 1000 which gives the value of the fresh root yield in tons per hectare. Top yield was calculated at harvest (12 MAP) by dividing the shoot weight per plot by the highest number of stands harvested per plot and multiplied by 12,000 divided by 1000 which gives the value of the top yield in tons per hectare. Dry yield was calculated at harvest (12 MAP) by dividing the value of fresh root yield by the value of the dry matter content multiplied by 100. The following traits: fresh root yield, dry yield, and top yield, were estimated in line with the protocol described by Hauser (2023) in the standard operating procedure for yield estimation in cassava. Harvest index was measured at harvest (12 MAP) as the ratio of fresh root weight to shoot weight per plot at harvest. In some cases, data collection was made for some of the traits across only four environments.

6.2.3 Statistical Analyses

Analysis of variance of the plant architecture and yield traits was performed using the `statgenGxE` package version 1.0 (van Rossum, 2022) of the R software (R Core Team, 2020). The mathematical formula of the adopted model is herein stated:

$Yijklm = \mu + Ei + R(E)\, j(i) + B(R\times E)\, k(ji) + Gl + (G\times E)il + \varepsilon ijklm$

Where:

Yijklm: observed yield for the m-th plot in block k, replicate j, environment i, and genotype l

μ: overall mean

Ei: random effect of i-th environment assumed $N(0,\sigma^2 E)$,

R(E)j(i): random effect of j-th replicate nested within the i-th environment $N(0,\sigma^2 R)$,

B(R×E)k (ji): random effect of k-th block nested within replicate j and environment i $N(0,\sigma^2 B)$,

Gl: fixed effect of l-th genotype,

(G×E)il : random effect of interaction between l-th genotype and i-th environment $N(0,\sigma^2 GE)$,

εijklm: is the random residual error, $N(0,\sigma^2\varepsilon)$.

The broad sense heritability (H^2) values were calculated as follows:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e^2}{er}}$$

Where H^2 is the broad sense heritability estimate, $\sigma^2 g$ is the genetic variance component of the accession effect, $\sigma^2 ge$ is the variance component of the genotype by environment effect, $\sigma^2 e$ is the variance component of the residual error, e is the number of environments and r is the number of replicates.

Stability and GEI analysis were performed using the Finlay-Wilkinson regression model in the `statgenGxE` package version 1.0 (van Rossum, 2022) of the R software (R Core Team, 2020) as described by (Malosetti *et al.*, 2013) while the Additive Main-effects and Multiplicative

Interaction (AMMI) model analysis was carried out according to the procedure described by (Gauch, 1992) and Genotype Main Effect plus Genotype Environment Interaction (GGE) analysis followed the protocol recommended by (Yan *et al*., 2000).

The mathematical formulae for the stability and GEI models are as follows:

Finlay-Wilkinson regression Model

$yij = \mu + Gi + \beta iEj + \epsilon ij$

yij - is the phenotypic value of genotype i in environment j

μ - is the general mean,

Gi - is the genotypic effect,

βi – the sensitivity parameter,

Ej – the environment effect

ϵij – the residual.

Additive Main-effects and Multiplicative Interaction (AMMI) Model

$yij = \mu + Gi + Ej + \sum\_(m = 1)\text{^}M\ \gamma mi\ \delta mj + \epsilon ij$

M - is number of principal components,

yij - is the phenotypic value of genotype i in environment j

μ - is the general mean,

Gi - is the genotypic effect,

Ej – the environmental effect,

γmi – the genotypic scores,

δmj – the environmental scores,

ϵij – the residual.

Genotype Main Effect plus Genotype Environment Interaction (GGE) Model

$yij = \mu + Ej + \gamma 1i\delta 1j + \gamma 2i\delta 2j + \epsilon ij$

yij - is the phenotypic value of genotype i in environment j

μ - is the general mean,

Ej – the environmental effect,

$\gamma 1i$ – the genotypic scores,

$\delta 1j$ – the environmental scores,

ϵij – the residual.

6.3 Results

6.3.1 Variance Components, Broad Sense Heritability and Genetic Advance of Plant Architecture and Yield Traits

Genotypic variance was higher than error variance for all the traits (Table 6.2). Pooled values of the broad sense heritability for all the traits studied in this trial were high; ranging from (0.71) for shoot weight to (0.89) for harvest index. The phenotypic and genotypic coefficient of variation ranged from 7.99% and 7.32% respectively for dry matter content to 29.12% and 25.67% respectively for fresh root yield (Table 6.2). The lowest value of genetic advance (0.19) was observed for harvest index while the highest value of 47.38 was recorded for plant height at 9 months after planting. The lowest value for genetic advance as a percentage of the mean 13.86 was realized from dry matter content while the highest value of 46.73 was recorded for fresh root yield (Table 6.2).

Table 6.1| Estimates of variance components, broad sense heritability, PCV, GCV, and genetic advance for plant architecture and yield traits in 453 cassava accessions evaluated across four/five environments in Nigeria.

Trait	Mean	σ^2_g	σ^2_{GxE}	σ^2_e	H^2	PCV(%)	GCV(%)	GA	GAM
STMDI9	22.3	4.36	0.57	0.85	0.76	10.78	9.36	3.75	16.8
FYLD	21.72	31.09	4.17	4.75	0.78	29.12	25.67	10.15	46.73
DYLD	7.8	3.28	0.48	0.57	0.76	26.67	23.22	3.26	41.74
STARCH	20.64	6.3	0.84	0.47	0.83	13.37	12.16	4.71	22.84
DM	33.42	5.99	0.67	0.47	0.84	7.99	7.32	4.63	13.86
RTWT	18.24	21.72	3.09	3.27	0.77	29.05	25.55	8.46	46.4
SHTWT	20.14	23.26	3.59	5.82	0.71	28.38	23.95	8.4	41.73
PLTHT9	181.44	608.9	30.79	64.6	0.86	14.63	13.6	47.38	26.11
HI	0.5	0.01	0	0	0.89	21.21	20	0.19	38.94
BRNHB9	2.5	0.15	0.02	0.02	0.77	17.61	15.49	0.7	28.15
ANGBR9	75.38	66.27	8.72	10.35	0.78	12.26	10.8	14.81	19.65

STMDI - stem diameter, FYLD - fresh root yield, DYLD - dry yield, STARCH – starch content, DM – dry matter content, RTWT – fresh root weight, SHTWT – shoot weight, PLTHT9 – plant height at 9 months after planting, LODG – number of lodged plants per plot, HI – harvest index, ANGBR9 – angle of branching, BRNHB9 – branching habit at 9 months after planting, $\sigma^2 g$ – genotypic variance, $\sigma^2 e$ – residual variance, $\sigma^2 p$ – phenotypic variance, H^2 - broad sense heritability, PCV, phenotypic coefficient of variation, GCV- genotypic coefficient of variation, GA - Genetic advance, GAM - genetic advance as a percentage of mean

6.3.2 Analysis of variance and genotypic performance

Combined ANOVA (Table 6.3) for the plant architecture traits: stem diameter, angle of branching, branching habit, harvest index, shoot weight, number of lodged plants per plot, plant height at 9 months after planting as well as yield traits root weight, fresh root yield, dry yield and quality traits: dry matter and starch content shows that all the factors: environment (E), genotype (G) and genotype by environment interaction (GEI) made immense contributions to the total phenotypic variations ($p < 0.001$) and were pivotal in determining the performance of the cassava accessions across the five environments. For all the traits except starch content, stem diameter and number of lodged plants per plot, variation due to the genotypic effect was responsible for most variation observed for these traits. The environmental effect caused the most variation observed on the first two traits while the effect imposed by the interaction between the genotype and environments was responsible for the major variation observed on the number of lodged plants per plot. Variation due to genotypic effects ranged from 15.76% for number of lodged plants per plot to 42.69% for branching habit. The cassava accessions expressed mixed performance in terms of the magnitude of the effect imposed by both the environmental factors and the interaction between genotype by environments. Observed variation due to effect of genotype by environment interaction falls between 15.41% for starch content and 35.18% for the number of lodged plants per plot. However, the highest variation due to the environmental effect 54.58% was recorded for starch content and the least was observed on branching habit 8.87 %.

Table 6.2|Output of combined ANOVA showing the mean square values and percentage contribution of all the factors to the total variation observed on all the plant architecture and yield traits across 4/5 environments.

	STDMI					ANGBR					BRHB					HI				
Source	DF	SS	MS	F	%TSS	DF	SS	MS	F	%TSS	DF	SS	MS	F	%TSS	DF	SS	MS	F	%TSS
ENV	3	31087.19	10362.4	1779.2***2	43.75	3	206597.75	68865.92	939.28***	30.44	3	135.04	45.01	260.15***	8.87	3	18.23	6.08	1275.26***	25.42
BLK(ENV*REP)	152	1809.125	11.90214	2.0***4	2.55	152	15665.93	103.07	1.41***	2.31	152	29.44	0.19	1.12	1.93	152	1.23	0.01	1.69***	1.71
REP(ENV)	4	421.2465	105.3116	18.08***	0.59	4	1215.19	303.80	4.14***	0.18	4	1.46	0.37	2.11*	0.10	4	0.63	0.16	33.3***	0.89
GEN	454	16682.84	36.74634	6.31***	23.48	449	212413.87	473.08	6.45***	31.29	454	649.71	1.43	8.27***	42.69	453	27.77	0.06	12.86***	38.72
GEN * ENV	1228	12463.25	10.14923	1.74***	17.54	1107	155498.64	140.47	1.92***	22.91	1247	437.04	0.35	2.03***	28.72	1340	14.67	0.01	2.3***	20.45
Residuals	1475	8590.605	5.82414		12.09	1192	87395.07	73.32		12.88	1556	269.24	0.17		17.69	1928	9.19	0.005		12.81
Total	3316	71054.26				2907	678786.5				3416	1521.9286				3880	72			
	SHTWT					LODG					PLTHT					DM				
Source	DF	SS	MS	F	%TSS	DF	SS	MS	F	%TSS	DF	SS	MS	F	%TSS	DF	SS	MS	F	%TSS
ENV	3	50216.07	16738.69	390.02***	13.78	4	2233.84	58.46	363.68***	18.81	3	1287114.34	429038.11	943.63***	23.54	4	20766.76	5191.69	1191.13***	27.21
BLK(ENV*REP)	152	10352.72	68.11	1.59***	2.84	190	313.4	1.65	1.07***	2.64	152	116386.07	765.70	1.68***	2.13	190	1482.32	7.80	1.79***	1.94
REP(ENV)	4	3102.51	775.63	18.07***	0.85	5	155.93	31.19	20.31***	1.31	4	89046.31	22261.58	48.96***	1.63	5	108.51	21.70	4.98***	0.14
GEN	453	116521.61	257.22	5.99***	31.98	454	1871.58	4.12	2.68***	15.76	453	2271565.09	5014.49	11.03***	41.54	454	26748.32	58.92	13.52***	35.05
GEN * ENV	1342	101363.37	75.53	1.76***	27.82	1697	4177.63	2.46	1.6***	35.18	1276	932475.11	730.78	1.61***	17.05	1663	18460.32	11.10	2.55***	24.19
Residuals	1930	82831.68	42.92		22.73	2033	3121.84	1.54		26.29	1697	771567.42	454.67		14.11	2006	8743.44	4.36		11.46
Total	3884	364388				4383	11874.22				3585	5468154				4322	76310			
	RTWT					STARCH					DYLD					FYLD				
Source	DF	SS	MS	F	%TSS	DF	SS	MS	F	%TSS	DF	SS	MS	F	%TSS	DF	SS	MS	F	%TSS
ENV	4	94471.70	23617.92	782.52***	22.86	4	52702.93	13175.73	2983.11***	54.58	4	5900.52	1475.13	279.92***	11.52	4	69038.12	17259.53	391.28***	13.23
BLK(ENV*REP)	190	9619.48	50.63	1.68***	2.33	190	1113.36	5.86	1.33***	1.15	190	1614.60	8.50	1.61***	3.15	190	12997.60	68.41	1.55***	2.49
REP(ENV)	5	2418.53	483.71	16.03***	0.59	5	165.63	33.13	7.5***	0.17	5	447.52	89.50	16.98***	0.87	5	3722.23	744.45	16.88***	0.71
GEN	454	125995.33	277.52	9.2***	30.48	449	21596.32	48.10	10.89***	22.37	454	16523.23	36.39	6.91***	32.26	454	177910.97	391.87	8.88***	34.10
GEN * ENV	1783	109305.37	61.30	2.03***	26.44	1218	14874.87	12.21	2.77***	15.41	1663	16205.76	9.74	1.85***	31.64	1783	153575.89	86.13	1.95***	29.43
Residuals	2370	71531.08	30.18		17.31	1381	6099.57	4.42		6.32	1999	10534.30	5.27		20.56	2370	104541.87	44.11		20.04
Total	4806	413341.5				3247	96553				4315	51225.938				4806	521786.68			

***, **, * significant at: 0.1%, 1% and 5% respectively

STDMI- stem diameter, ANGBR- angle of branching, BRHB- branching habit, HI- harvest index, SHTWT- shoot weight, LODG- number of lodged plants per plot, PLHT- plant height at 9 months after planting, RTWT- root weight, FYLD- fresh root yield, DYLD- dry yield, DM- dry matter and STARCH- starch content.

6.3.3 Genotype Main Effects and Genotype by Environment Interaction (GGE) Model

The output of the GGE model (Table 6.4) for combined analysis of all the traits: plant architecture: stem diameter, angle of branching, branching habit, harvest index, shoot weight, number of lodged plants per plot, plant height at 9 months after planting as well as yield traits root weight, fresh root yield, dry yield and quality traits: dry matter and starch content showed there is significant environment effect ($p < 0.001$) for all the traits, as well as effect that was due to genotype by environment interaction ($p < 0.001$), (Table 6.4). Interaction by genotype and environment accounted for the large portion of the total phenotypic variation observed for all the traits, except on stem diameter and starch content where it only accounted for 31.38 % and 21.25 % respectively. Meanwhile, the highest value 46.69 %, was observed for branching habit. The contributions in respect of environment ranged between 6.62% on branching habit to 57.51% from starch content.

Table 6.3|ANOVA table for the GGE model showing the percentage contribution of all the factors to the total variation and percentage of GGE variation observed on all the plant architecture and yield traits across 4/5 environments.

	STMDI					ANGBR					BRHB					HI				
Source	DF	SS	F	%TSS	%GGE	DF	SS	F	%TSS	%GGE	DF	SS	F	%TSS	%GGE	DF	SS	F	%TSS	%GGE
Env	3	21531.8	718***	37.24		3	190952	436***	26.7		3	79.4	85.8***	6.62		3	9.75	269.7***	18.28	
G+GE	1816	18145.7		31.38		1796	262177		36.65		1816	560		46.69		1812	21.8		40.86	
PC1	457	11997.8	8.4***	20.75	66.12	452	163257	6.8***	22.82	62.27	457	338.8	5.5***	28.25	60.5	456	14.7	7.5***	27.55	67.43
PC2	455	3330.5	2.3***	5.76	18.35	450	51286	2.3***	7.17	19.56	455	99.9	1.6***	8.33	17.84	454	3.2	1.6***	6	14.68
Residuals	904	2817.4		4.87		894	47633		6.66		904	121.3		10.11		902	3.9		7.31	
Total		57823.2					715305					1199.4					53.35			
	SHTWT					LODG					PLTHT					DM				
Source	DF	SS	F	%TSS	%GGE	DF	SS	F	%TSS	%GGE	DF	SS	F	%TSS	%GGE	DF	SS	F	%TSS	%GGE
Env	3	32064	174***	12.6		4	777.2	129***	10.24		3	951206	357***	22.83		4	13083.9	286.2***	20.14	
G+GE	1812	111206		43.7		2270	3407.5		44.88		1812	1608007		38.59		2270	25947.2		39.93	
PC1	456	61032	4.5***	23.98	54.88	458	2155.7	9.7***	28.39	63.26	456	1213954	12***	29.13	75.49	458	17682	10.4***	27.21	68.15
PC2	454	23267	1.7***	9.14	20.92	456	594.8	2.7***	7.83	17.46	454	193506	1.9***	4.64	12.03	456	3245.2	1.9***	4.99	12.51
Residuals	902	26907		10.57		1356	656.9		8.65		902	200547		4.81		1356	5020		7.73	
Total		254476					7592.1					4167220					64978.3			
	RTWT					STARCH					DYLD					FYLD				
Source	DF	SS	F	%TSS	%GGE	DF	SS	F	%TSS	%GGE	DF	SS	F	%TSS	%GGE	DF	SS	F	%TSS	%GGE
Env	4	54846	256***	18.42		4	70187	1519***	57.51		4	4620	140.3***	11		4	41614	137.5***	10.81	
G+GE	2270	121414		40.79		2245	25930		21.25		2270	18694		44.5		2270	171754		44.6	
PC1	458	69513	6.4***	23.35	57.25	453	16608	8.7***	13.61	64.05	458	10256	5.6***	24.41	54.86	458	94916	5.7***	24.65	55.26
PC2	456	19834	1.8***	6.66	16.34	451	3669	1.9***	3.01	14.15	456	3012	1.7***	7.17	16.11	456	27749	1.7***	7.21	16.16
Residuals	1356	32067		10.77		1341	5652		4.63		1356	5426		12.92		1356	49090		12.75	
Total		297674					122046					42008					385123			

***, **, * significant at: 0.1%, 1% and 5% respectively

STDMI- stem diameter, ANGBR- angle of branching, BRHB- branching habit, HI- harvest index, SHTWT- shoot weight, LODG- number of lodged plants per plot, PLHT- plant height at 9 months after planting, RTWT- root weight, FYLD- fresh root yield, DYLD- dry yield, DM- dry matter and STARCH- starch content.

The GGE biplot analysis revealed substantial genotype × environment interactions (GEI) for fresh root yield (FYLD), plant height (PLTHT) and starch content (STARCH) respectively; principal component analysis of the GGE biplot showed that PC1 and PC2 together explained 78.1% of the total GGE variation (PC1 = 64.2 %, PC2 = 13.9%) for fresh root yield and 84.8% of the total GGE variation (PC1 = 75.4%, PC2 = 9.4%) for starch content indicating a reliable visualization of the genotype and environment relationships.

Discriminating Ability and Representativeness of Test Environments

The biplots for fresh root yield (FYLD) (Figure 6.1and starch content (STARCH) (Figure 6.2), revealed considerable variation in the discriminating ability and representativeness of the test environments. Environments with longer vectors from the biplot origin exhibited stronger discriminating power for genotypic differences; the outputs showed varied unpredictable patterns across environments for the three traits under review. Among these, (IK20) and Ikenne 19 (IK19) formed relatively smaller angles with the average environment axis (horizontal red line) across all the traits, indicating higher representativeness of the overall testing network.

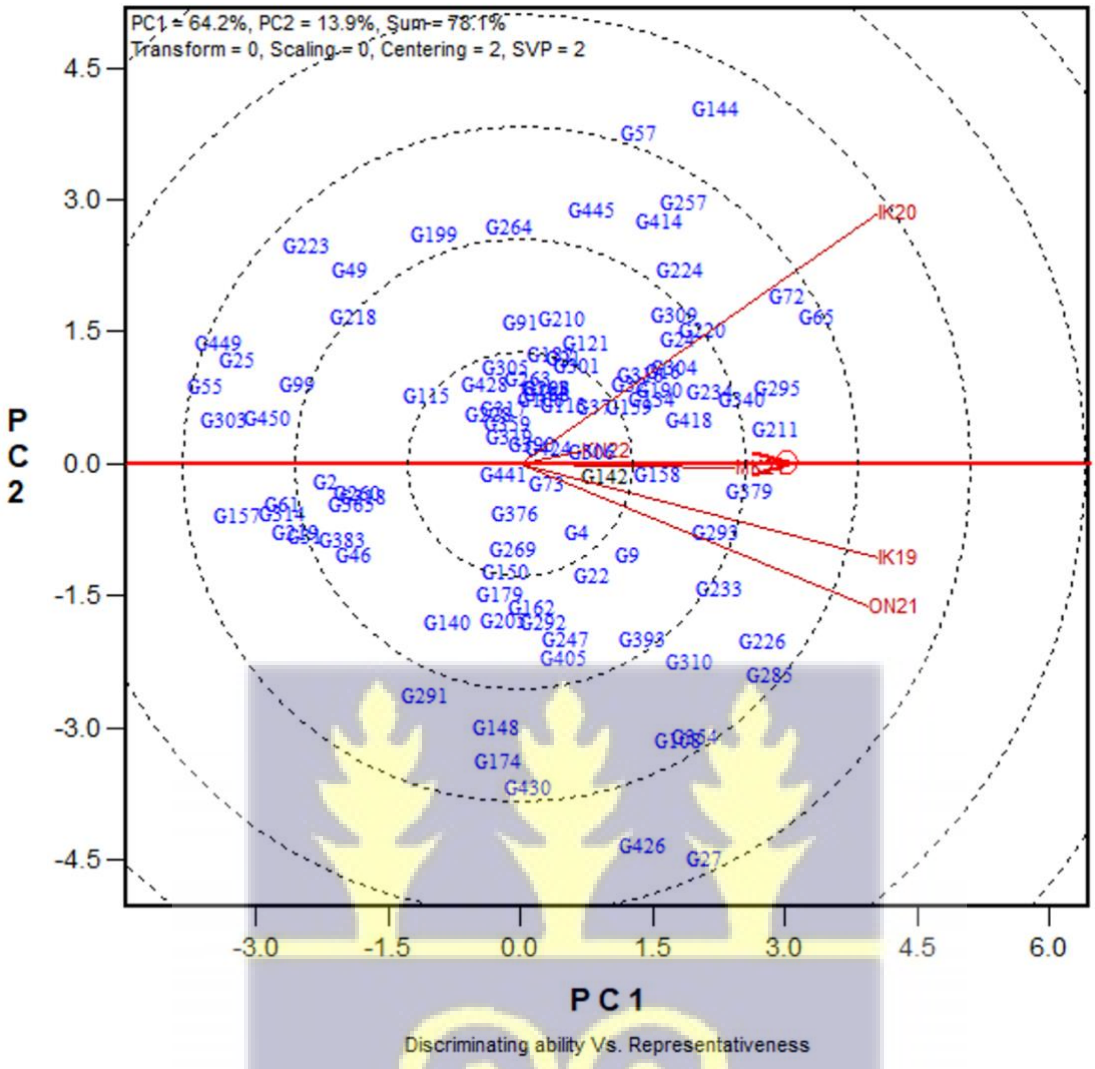

Figure 6.1| Assessment of test environments for representativeness and discrimination for FYLD across five testing environments.

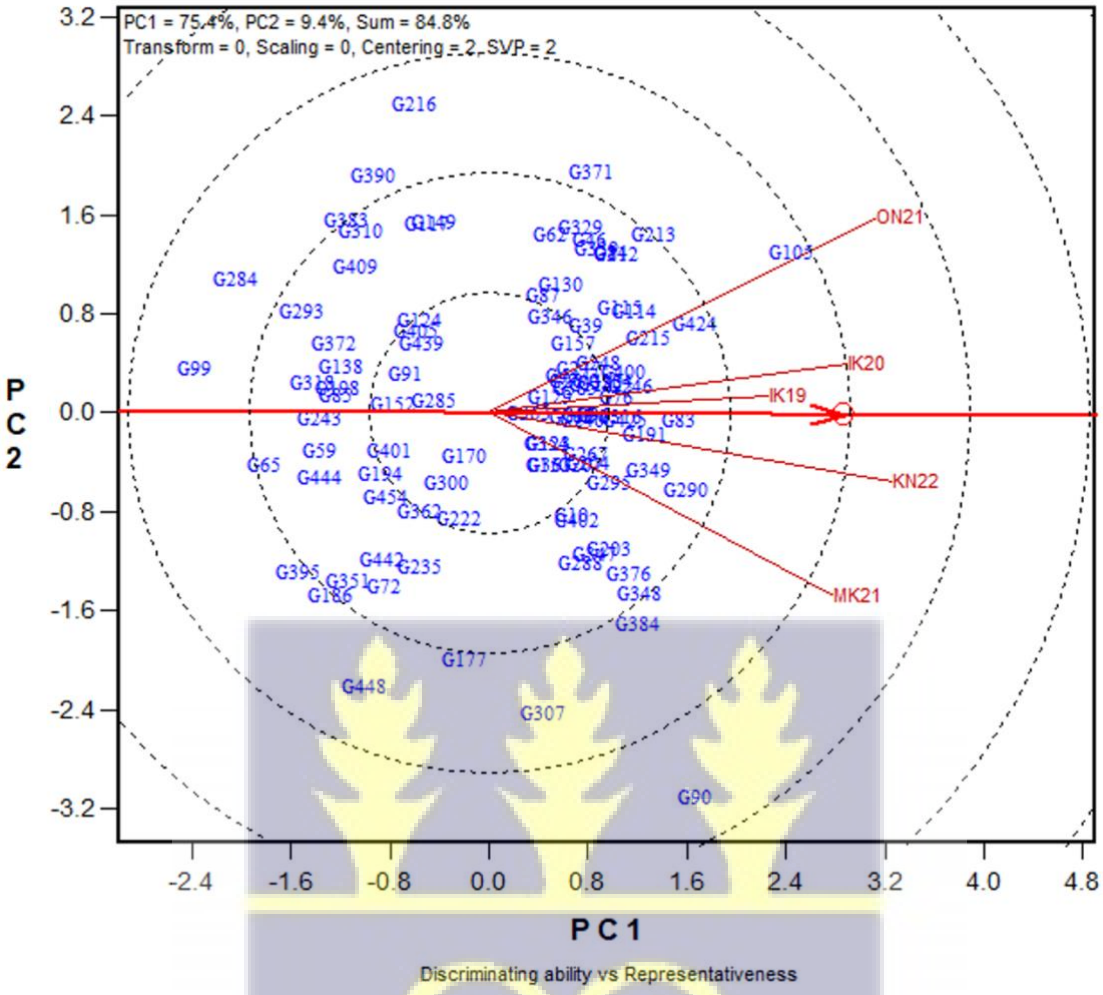

Figure 6.2| Assessment of test environments for representativeness and discrimination for STARCH across five testing environments

Identification of Winning Genotypes and Mega-environments

The polygon view of the GGE biplots for FYLD (Figure 6.3) and STARCH (Figure 6.4) partitioned the testing environments into distinct sectors, effectively identifying the "which-won-where" pattern. Genotypes positioned at the vertices of the polygon exhibited the most extreme responses across environments. The clustering of environments in one sector indicates a potential mega-environment where certain genotypes demonstrated superior adaptation; IK19 was observed to be consistently clustered with a couple of potentially distinctive mega environment across traits.

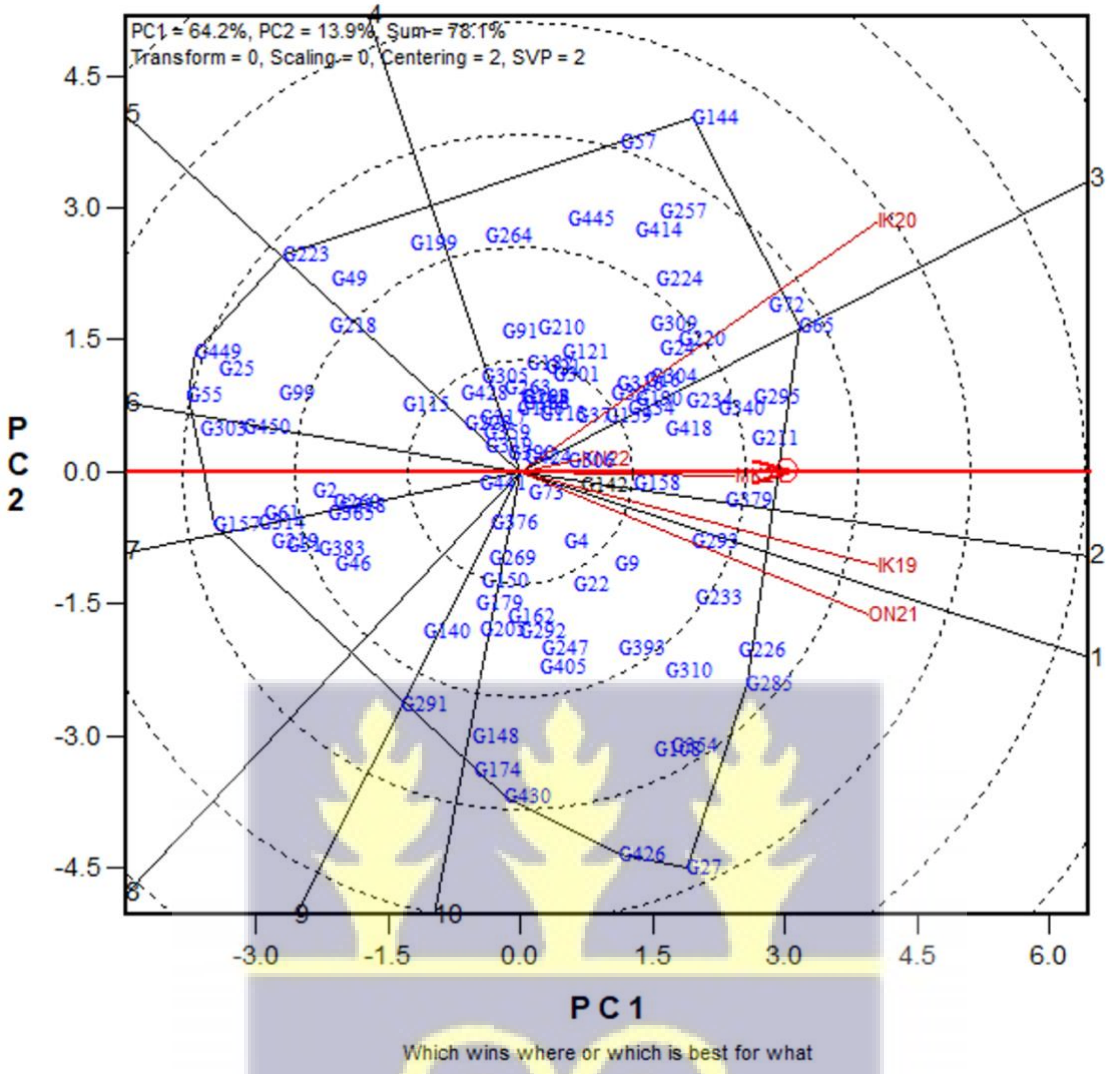

Figure 6.3| Identification of winning genotypes and mega-environments for FYLD across five testing environments.

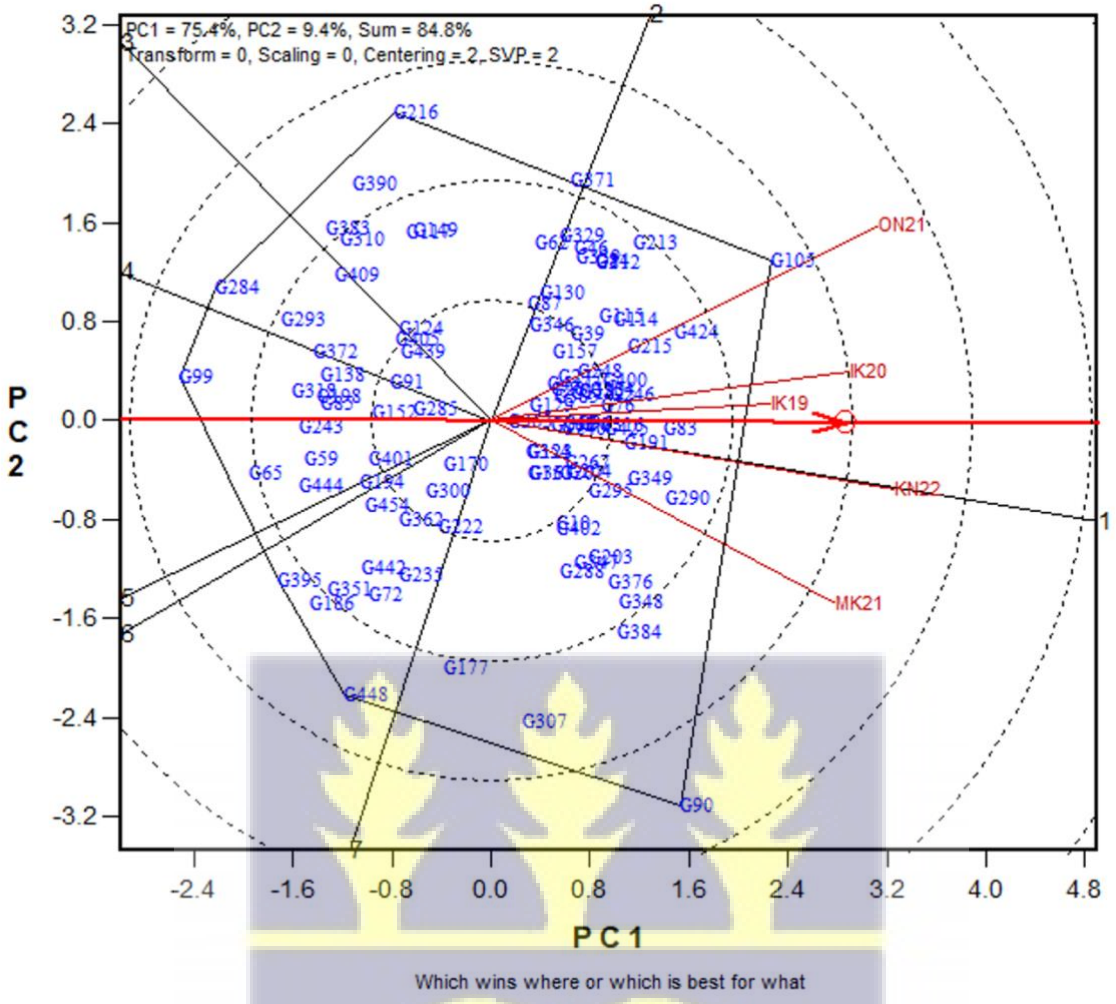

Figure 6.4| Identification of winning genotypes and mega-environments for STARCH across five testing environments.

Evaluation of Ideal Testing Environment

Figures 6.5, and 6.6 illustrate the ranking of test environments relative to an "ideal environment" (represented by the small circle on the positive PC1 axis). The environments Mokwa 21 (MK21) and Ikenne 19 (IK19) positioned closest to the ideal environment demonstrated the optimal balance between discriminating ability and representativeness for FYLD and STARCH respectively.

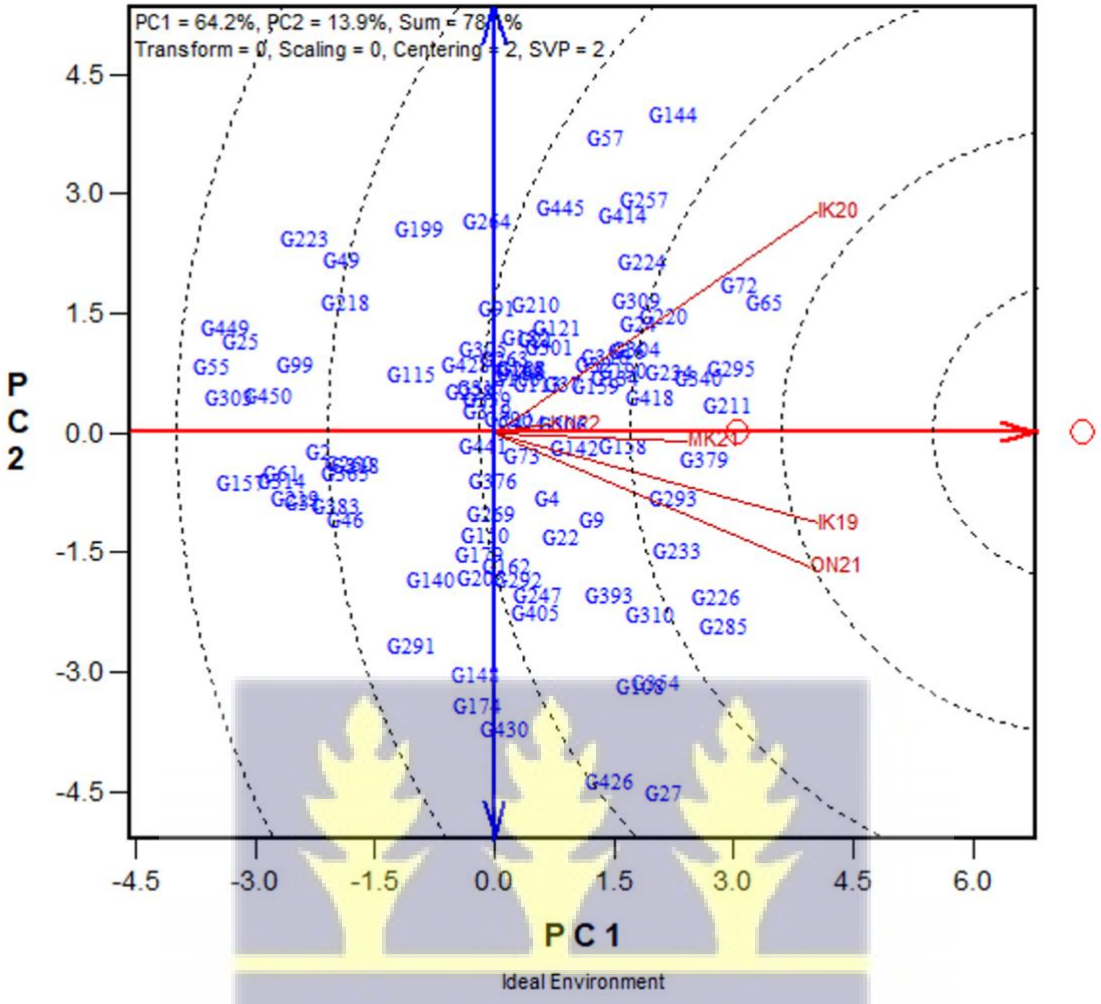

Figure 6.5| Evaluation of ideal testing environment for FYLD across five testing environments.

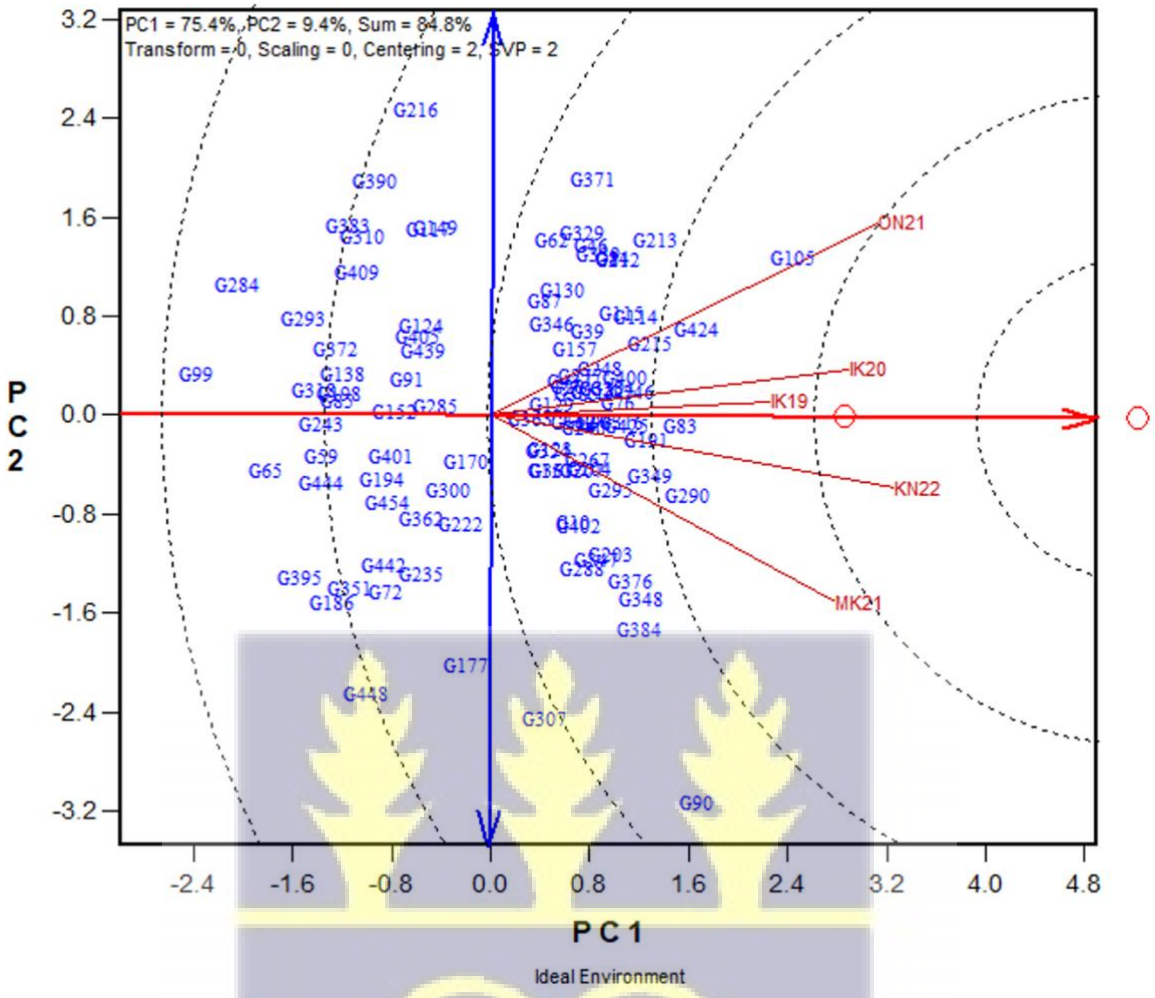

Figure 6.6| Evaluation of ideal testing environment for STARCH across five testing environments.

Identification of Superior Genotypes

The evaluation of genotypes relative to the conceptual "ideal genotype" (Figure 6.7 & 6.8) identified several promising accessions with both high performance and stability across environments. Genotypes positioned closer to the ideal genotype marker on the positive PC1 axis, particularly G418 (TMS18F1414P0017), G159 (TMS18F1260P0060) and G234 (TMS18F1313P0053) combined above-average yield performance with relative stability across diverse environments for FYLD, while genotypes G83 (TMS18F1096P0013), G424 (TMS18F1436P0049) and G215 (TMS18F1306P0127) were outstanding for STARCH. The fresh root yield of these genotypes ranged from 21.14 t/ha to 30.72 t/ha for G424 (TMS18F1436P0049) and G83 (TMS18F1096P0013) respectively. However, G424 (TMS18F1436P0049) had the highest starch content 25.39% followed by G83 (TMS18F1096P0013) with 25.28%. These two genotypes also have erect plant type that is suitable for mechanized cultivation (Table 6.5).

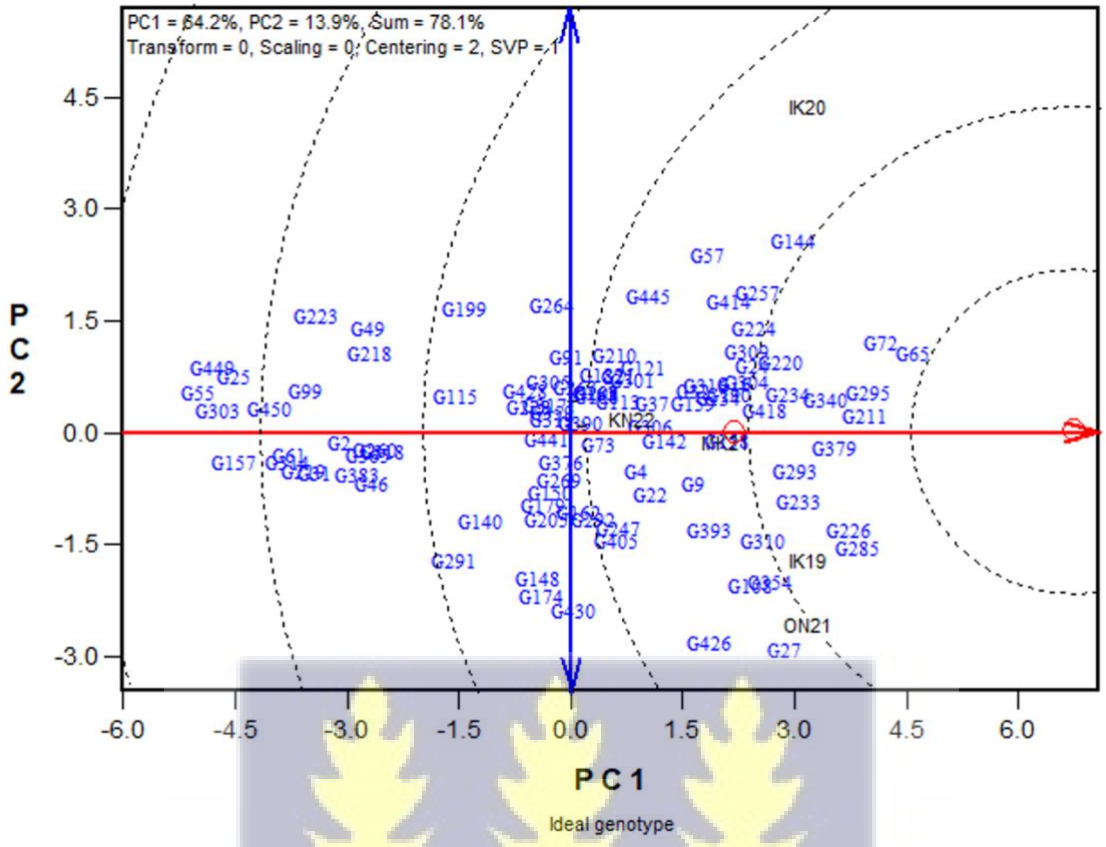

Figure 6.7 | Identification of superior genotypes for FYLD across five testing environments.

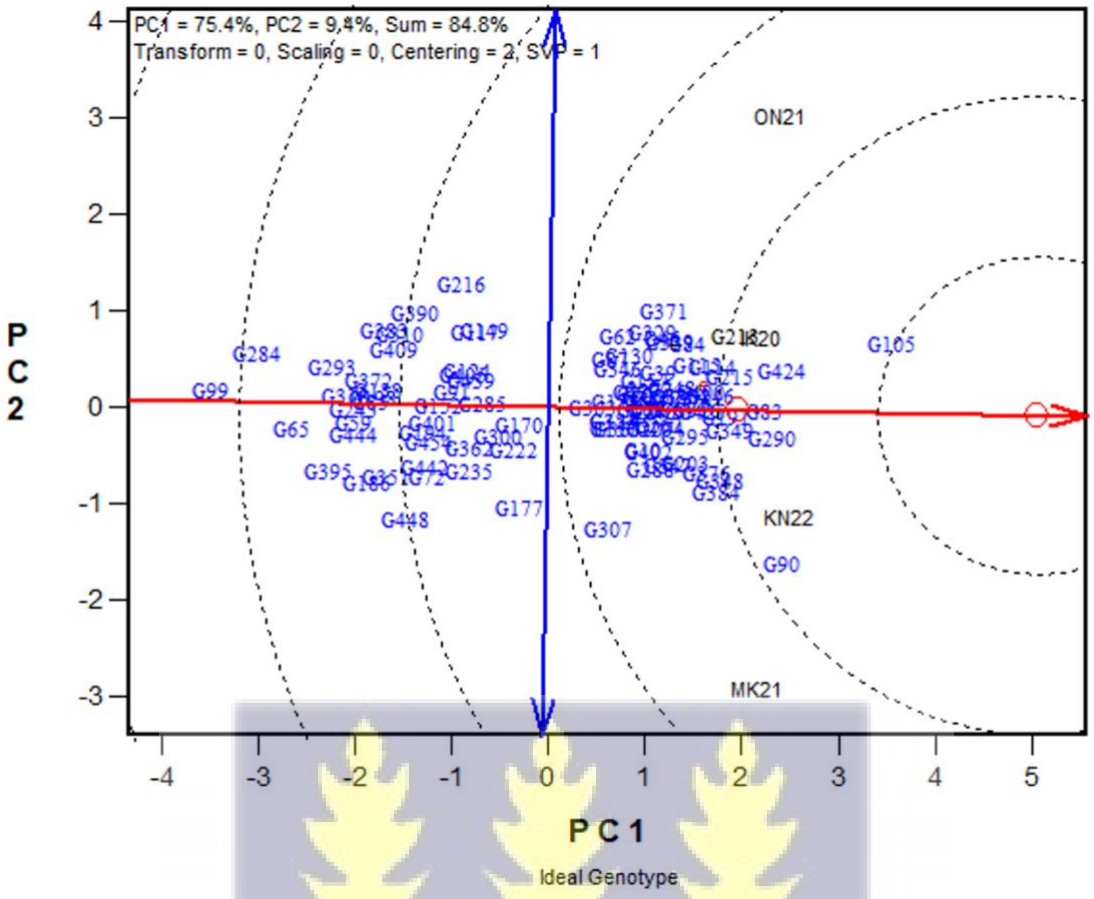

Figure 6.8| Identification of superior genotypes for STARCH across five testing environments.

Table 6.4|Features of the best performing genotypes for fresh root yield and starch contents across 5 environments

Accession Name	Gen	PT	FYLD	STARCH	DM	RTWT	DYLD	PLTHT	LODG	SHTWT	HI	BRNHB	ANGBR	STMDI
TMS18F1414P0017	G418	3	26.33	21.24	33.25	22.22	9.04	173.73	1	21.84	0.56	3	64.46	21.12
TMS18F1260P0060	G159	3	25.58	21.22	33.84	21.56	9.23	142.18	0	13.64	0.63	3	83.03	18.74
TMS18F1313P0053	G234	3	29.98	24.77	37.37	24.94	11.29	184.15	1	22.46	0.56	3	80.59	24.64
TMS18F1096P0013	G83	1	30.72	25.28	37.40	26.61	11.52	189.38	1	26.00	0.53	3	87.02	21.30
TMS18F1436P0049	G424	1	21.14	25.39	38.05	17.93	8.85	160.08	1	15.27	0.58	3	73.61	18.21
TMS18F1306P0127	G215	3	29.84	28.19	38.35	25.23	11.46	210.17	2	24.65	0.53	3	71.34	27.18

Gen – Genotypye ID, PT – Plant Type (1- erect, 2 – umbrella, 3 – compact and 4 – open)
STDMI- stem diameter, ANGBR- angle of branching, BRHB- branching habit, HI- harvest index, SHTWT- shootweight, LODG- number of lodged plants per plot, PLHT- plant height at 9 months after planting, RTWT- root weight, FYLD- fresh root yield, DYLD- dry yield, DM- dry matter and STARCH- starch content.

6.3.4 Additive Main Effects and Multiplicative Interaction (AMMI) Model

The ANOVA table for AMMI model of the combined analysis of all the traits: plant architecture: stem diameter, angle of branching, branching habit, harvest index, shoot weight, number of lodged plants per plot, plant height at 9 months after planting as well as yield traits root weight, fresh root yield, dry yield and quality traits: dry matter and starch content shows that the effects for both the genotype, and environment and their interaction made significant contributions ($P < 0.001$) to the total phenotypic variation observed for all the traits. The interaction between genotypes and environments were decomposed into interaction principal component 1 (IPCA1), and interaction principal component 2 (Table 6.5). The genotypic main effect accounted for most of the total phenotypic variance in all the traits except for stem diameter, angle of branching, number of lodged plants per plot, starch and dry yield where the environmental main effects accounted for most of the observed total phenotypic variation with the exception of the number of lodged plants per plot where the interaction between the genotype and environment had a slightly higher value 33.75 %. The contributions of the genotypic main effect to the total phenotypic variation ranged between 15.47% for starch and 39.49% in plant height at 9 months after planting.

The first principal component (IPC1) and second principal component (IPC2) explained 58.68% and 24.41% respectively, of the total GE variance (83.09%), in the AMMI analysis for stem diameter (Table 6.5). The cumulative value of 83.09% was the highest for all the traits. However, the first two IPCs for dry yield contributed 34.50% and 29.99% respectively to the variation observed in the total sum of squares with a cumulative value of 64.49% which was the least cumulative value recorded amongst all the traits. The total sum of squares variation accounted for by the IPCs ranged from 3.21% for IPC2 in starch content and 17.22% for IPC1 in the number of lodged plants per plot.

Table 6.5| The ANOVA table of the AMMI model of the combined analysis for all the plant architecture and yield traits that depicts percentage contributions of each factor and principal component to the total phenotypic variation across 4/5 environments.

	STMDI					ANGBR					BRHB					HI				
Source	DF	SS	F	%TSS	%GE	DF	SS	F	%TSS	%GE	DF	SS	F	%TSS	%GE	DF	SS	F	%TSS	%GE
Env	3	21531.8	1235.5***	45.24		3	190952	755.8***	33.7		3	79.4	150.1***	9.03		3	9.75	583.8***	24.89	
Gen	454	10233.4	3.8***	21.5		449	148738	3.9***	26.25		454	319.94	4.0***	36.38		453	14.28	5.7***	36.46	
GE	1362	7912.3		16.63		1347	113439		20.02		1362	240.06		27.3		1359	7.57		19.33	
PC1	456	4642.9	3.4***	9.76	58.68	451	57223	2.7***	10.1	50.44	456	107.07	2.1***	12.17	44.6	455	3.61	2.1***	9.22	47.69
PC2	454	1931.6	1.4***	4.06	24.41	449	34962	1.6***	6.17	30.82	454	82.27	1.6***	9.35	34.27	453	2.28	1.4***	5.82	30.12
Residuals	452	1337.8		2.81		447	21254		3.75		452	50.72		5.77		451	1.68		4.29	
Total		47589.8					566568					879.46					39.17			
	SHTWT					LODG					PLTHT					DM				
Source	DF	SS	F	%TSS	%GE	DF	SS	F	%TSS	%GE	DF	SS	F	%TSS	%GE	DF	SS	F	%TSS	%GE
Env	3	32064	277.8***	16.4		4	777.23	165.5***	12.31		3	951206	1006***	31.84		4	13083.9	568.6***	26.44	
Gen	453	58922	3.4***	30.13		454	1275.95	2.4***	20.2		453	1179810	8.3***	39.49		454	15501.1	5.9***	31.33	
GE	1359	52284		26.74		1816	2131.56		33.75		1359	428197		14.33		1816	10446.1		21.11	
PC1	455	23335	2.2***	11.93	44.63	457	1087.5	4.7***	17.22	51.02	455	200505	2.2***	6.71	46.83	457	5401.1	3.7***	10.92	51.7
PC2	453	18765	1.8***	9.6	35.89	455	586.86	2.6***	9.29	27.53	453	138030	1.5***	4.62	32.24	455	2153.8	1.5***	4.35	20.62
Residuals	451	10185		5.21		904	457.21		7.24		451	89662		3		904	2891.2		5.84	
Total		195555					6316.31					2987410					49477.2			
	RTWT					STARCH					DYLD					FYLD				
Source	DF	SS	F	%TSS	%GE	DF	SS	F	%TSS	%GE	DF	SS	F	%TSS	%GE	DF	SS	F	%TSS	%GE
Env	4	54846	426.8***	23.38		4	70187	3289.3***	66.4		4	4620.9	219.4***	14.05		4	41614	231.5***	14.11	
Gen	454	63077	138.9***	26.89		449	16349	6.8***	15.47		454	9131.2	3.8***	27.77		454	90152	4.4***	30.56	
GE	1816	58336		24.87		1796	9581		9.06		1816	9563		29.09		1816	81602		27.66	
PC1	457	23905	2.5***	10.19	40.98	452	3669	2.9***	3.47	38.29	457	3299.3	1.9***	10.03	34.5	457	28385	2***	9.62	34.78
PC2	455	15216	1.6***	6.49	26.08	450	3396	2.7***	3.21	35.45	455	2868.3	1.7***	8.72	29.99	455	24497	1.7***	8.3	30.02
Residuals	904	19216		8.19		894	2516		2.38		904	3395.4		10.33		904	28721		9.74	
Total		234596					105698					32878.1					294971			

***, **, * significant at: 0.1%, 1% and 5% respectively

STDMI- stem diameter, ANGBR- angle of branching, BRHB- branching habit, HI- harvest index, SHTWT- shoot weight, LODG- number of lodged plants per plot, PLHT- plant height at 9 months after planting, RTWT- root weight, FYLD- fresh root yield, DYLD- dry yield, DM- dry matter and STARCH- starch content.

The polygon view of the AMMI 2 biplots Figures 6.9 and 6.10, revealed that the PC 1 (34.8%) and PC 2 (30%) accounted for 64.8% of all the total variation observed for fresh root yield while PC 1 (38.3%) and PC 2 (35.4%) captured about 73.7% of the total variation observed for the starch content. The AMMI polygon plot (Figure 6.9) also showed that there exist strong positive relationships between the test environments Mokwa (MK22) and Kano (KN23), likewise between test environments Ikene (IK20), and Onne (ON22) for fresh root yield, while the test environment Ikene (IK21) stood alone.

In the same vein, in Figure 6.10, the test environment Onne (ON22) had a distinct influence on the performance of genotypes in respect of starch content while test environments Ikene (IK21) and Ikene (IK20) exhibit a strong positive correlation in their effect on the genotypes in respect of the quantity of starch they produced.

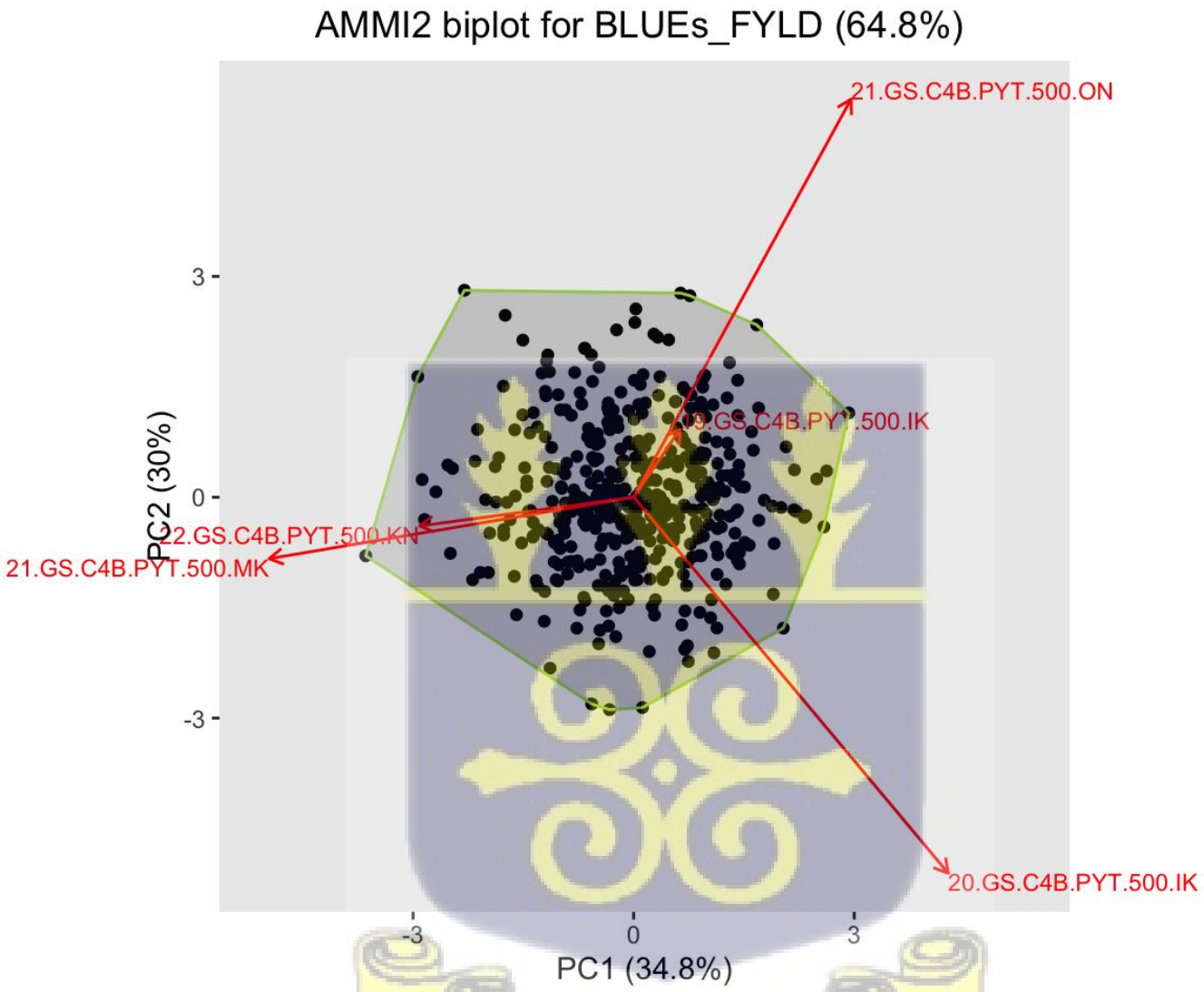

Figure 6.9| The polygon view of the AMMI 2 biplot for fresh root yield across the test environments

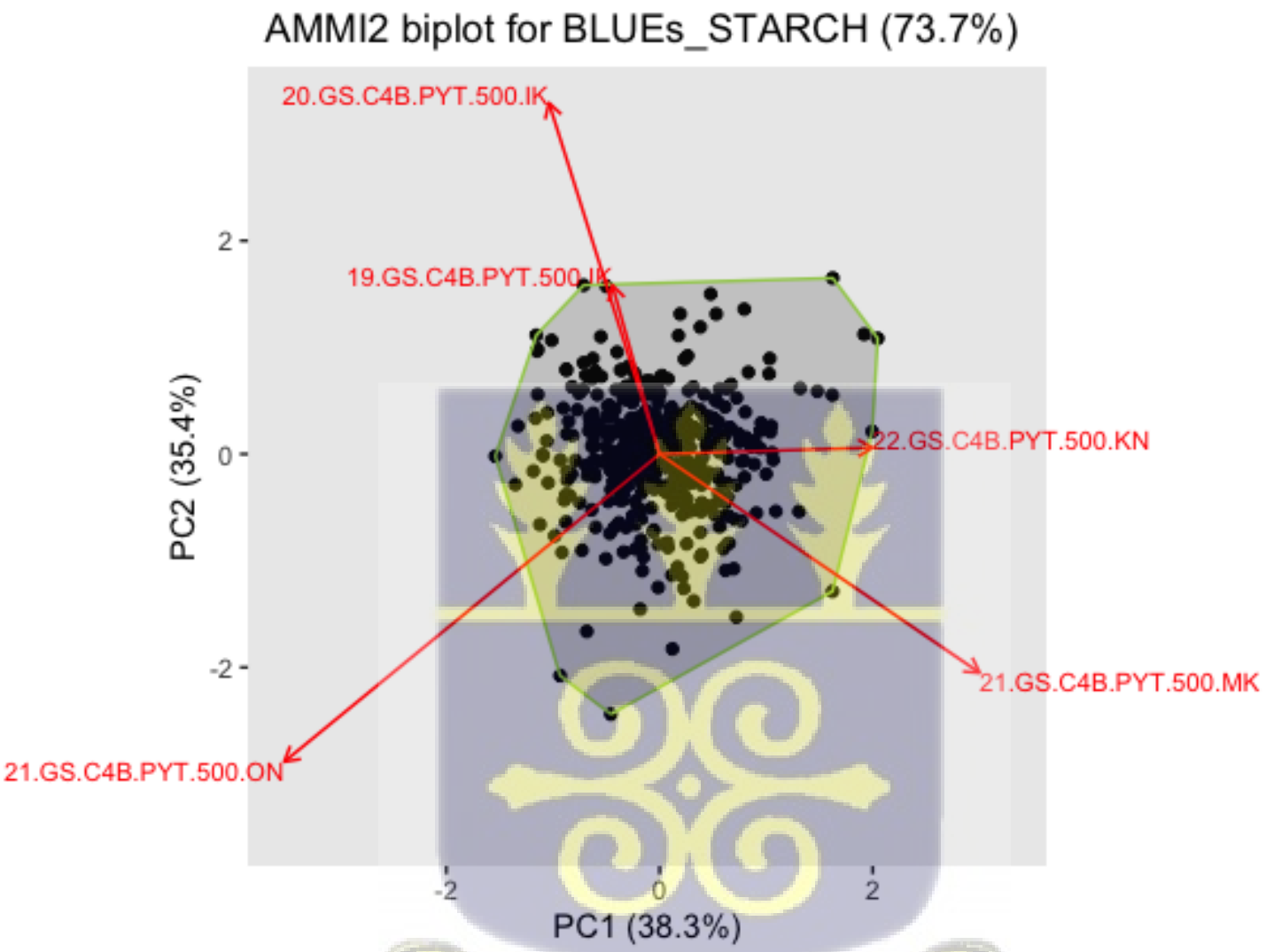

Figure 6.10| The polygon view of the AMMI 2 biplot for starch content across the test environments

Table 6.6| The AMMI analysis delineation of the test environments into MEGA Environments and the winning genotypes

MEGA Environment	PLTHT Winning Genotype	MEGA Environment	LODG Winning Genotype	MEGA Environment	SHTWT Winning Genotype	MEGA Environment	HI Winning Genotype
IK 20	G130	IK 20	G25	MK 22	G413	ON 22	G291
MK 22	G384	IK 21	G251	IK 21	G446	IK 21	G437
IK 21	G416	MK 22	G345	ON 22	G455	MK 22	G55
ON 22	G455	ON 22	G81	IK 20	G50	IK 20	G59
		KN 23	G96				
MEGA Environment	ANGBR Winning Genotype	MEGA Environment	STMDI Winning Genotype	MEGA Environment	BRHB Winning Genotype	MEGA Environment	DM Winning Genotype
ON 22	G185	ON 22	G172	IK 21	G16	IK 20, IK21, KN 23, ON 22	G105
IK 21	G211	MK 22, KN 23	G26	MK 22	G41	MK 22	G453
KN 23	G214	IK 21	G390	ON 22	G36		
MK 22	G236			KN 23	G85		
MEGA Environment	FYLD Winning Genotype	MEGA Environment	STARCH Winning Genotype	MEGA Environment	RTWT Winning Genotype	MEGA Environment	DYLD Winning Genotype
IK 20	G58	IK 20 & IK 21	G105	IK 20	G58	IK 21	G295
IK 21	G59	MK 22 & KN 23	G133	IK 21	G59	MK 22 & KN 23	G72
MK 22 & KN 23	G72	ON 22	G329	MK 22 & KN 23	G72	IK 20 & ON 22	G83
ON 22	G83			ON 22	G83		

IK 20 – Ikenne 2020 trial, IK 21- Ikenne 2021 trial, MK 22- Mokwa 2022 trial, ON 22-, Onne 2022 trial and KN 23- Kano 2023 trial.

6.3.5 Finlay-Wilkinson model

The output of the Finlay-Wilkinson model analysis (Table 6.7) for all the traits of plant architecture: stem diameter, angle of branching, branching habit, harvest index, shoot weight, number of lodged plants per plot, plant height at 9 months after planting as well as yield traits root weight, fresh root yield, dry yield and quality traits: dry matter and starch content revealed significant effects ($p< 0.001$) for both genotype and environment main effects. However, considering the differential response of the genotypes to changes in the environment mean which is a function of sensitivity, only four traits were observed to display sensitivity: dry matter content, number of lodged plants per plot, shoot weight ($p < 0.001$), and root weight ($p < 0.01$). The genotypes were indifferent in their responses to the changes in the environmental mean for the remaining traits.

Table 6.7| The ANOVA table of the Finlay-Wilkinson model of the combined analysis for all the plant architecture and yield traits that depicts percentage contributions of each factor and sensitivity to the total phenotypic variation across 4/5 environments.

	STMDI				ANGBR				BRHB				HI			
Source	DF	SS	F	TSS (%)	DF	SS	F	TSS (%)	DF	SS	F	TSS (%)	DF	SS	F	TSS (%)
Environment	3	18741	364.6***	50.21	3	138778	353.7***	32.76	3	76.5	129.3***	12.24	3	9.63	518***	30.8
Genotype	454	10918	1.4***	29.25	449	180274	3.1***	42.55	454	3115.1	3.5***	498.3	453	14.09	5***	45.06
Sensitivity	454	-5598		-15	449	18584	1	4.39	454	77.06	0.9	12.33	453	2.5	0.7	7.99
Residuals	774	13262		35.53	658	86048		20.31	793	156.47		25.03	887	5.5		17.59
Total	1685	37323			1559	423683			1704	625.14			1796	31.27		
	SHTWT				LODG				PLTHT				DM			
Source	DF	SS	F	TSS (%)	DF	SS	F	TSS (%)	DF	SS	F	TSS (%)	DF	SS	F	TSS (%)
Environment	3	31437	332.4***	22.06	4	648	154.1***	15.72	3	851180	665.2***	35.05	4	12163	531.7***	32.23
Genotype	453	58823	4.1***	41.29	454	1364.5	2.9***	33.09	453	1155348	6***	47.58	454	15350	5.9***	40.67
Sensitivity	453	24193	1.7***	16.98	454	867.6	1.8***	21.04	453	70762	1	2.91	454	3315	1.3***	8.78
Residuals	889	28024		19.67	1183	1243.3		30.15	823	351014		14.46	1209	6914		18.32
Total	1798	142477			2095	4123.3			1732	2428304			2121	37742		
	RTWT				STARCH				DYLD				FYLD			
Source	DF	SS	F	TSS (%)	DF	SS	F	TSS (%)	DF	SS	F	TSS (%)	DF	SS	F	TSS (%)
Environment	4	54799	442.8***	31.48	4	35429	388***	55.61	4	4568.5	199.7***	20.56	4	41831	212.8***	19.82
Genotype	454	61510	4.4***	35.33	449	19406	1.9***	30.46	454	8527.8	3.3***	38.38	454	88259	4***	41.81
Sensitivity	454	16665	1.2*	9.57	449	-8687		-13.64	454	2208.8	0.9	9.94	454	15666	0.7	7.42
Residuals	1329	41119		23.62	769	17556		27.56	1209	6912.8		31.11	1329	65322		30.95
Total	2241	174092			1671	63705			2121	22217.8			2241	211077		

***, **, * significant at: 0.1%, 1% and 5% respectively

STDMI- stem diameter, ANGBR- angle of branching, BRHB- branching habit, HI- harvest index, SHTWT- shoot weight, LODG- number of lodged plants per plot, PLHT- plant height at 9 months after planting, RTWT- root weight, FYLD- fresh root yield, DYLD- dry yield, DM- dry matter and STARCH- starch content.

6.4 Discussion

The prospect of a germplasm or breeding population for genetic improvement is a function of the contribution of the genetic components to the total observed variation and the overall effect of the environment and its interaction with the genotypes on the performance of the measured traits. All the plant architecture and yield traits measured across the five environments, including stem diameter, angle of branching, branching habit, harvest index, shoot weight, number of lodged plants per plot, plant height at 9 months after planting, root weight, fresh root yield, dry yield, dry matter, and starch content were significantly influenced by genotype, environment, and the interaction between genotype and environment. The genotypic components had higher impacts in respect of the overall variations observed for all the traits, except starch content, stem diameter, angle of branching and number of lodged plants per plot. This is an indication that this population could be effectively improved for these traits through conventional breeding procedures viz: hybridization and selection (Schmidt, Hartung, Bennewitz, & Hans-Peter, 2019).

Several studies have shown that cassava genotypes produced differential expressions in terms of yield and plant architecture traits in response to varying environmental variables (Manu-Aduening *et al*., 2013; Adjebeng-Danquah *et al*., 2017; Nduwumuremyi *et al*., 2017; Chipeta *et al*., 2018; Adjebeng-danquah *et al*., 2020a; Jiwuba *et al*., 2020; Bakare *et al*., 2022). This phenomenon is often referred to as genotype-by-environment (GEI) interaction. One of the major challenges in the crop breeding program is the presence of genotype by environment interaction (GEI). It reduces the genetic advance due to decreasing genotypic-phenotypic correspondence. The presence of significant GEI disrupts the trends in the observable variation and performance pattern of the breeding population, thereby leading to inconsistency in the selection of best-yielding material across trial environments and create a bottleneck in cultivar recommendation. This problem demands breeders to test their material in multiple test environments to determine the suitability of cultivation of the chosen genotypes across environments (Zakir, 2018). In the research conducted by Adjebeng-danquah *et al*. (2020a), they observed that the environment, genotypes, and interaction between the two had a significant impact ($p < 0.001$) on the manner of expression of the root yield, plant height and harvest index. Bakare *et al*. (2022), also reported similar results for fresh root yield, dry yield, top yield, dry matter content and harvest index in cassava.

Genotype-by-environment interaction (GEI) is a function of the performance of genotypes in relation to the test environments. It confounds the selection decision of breeders in recommending superior genotypes. Its real effects on the stability of genotypes and delineation of test environments into mega environments could be analysed using statistical models such as AMMI (Additive Main Effects and Multiplicative Interaction), Finlay-Wilkinson, and GGE (Genotype Main Effects and Genotype by Environment Interaction) biplots. Based on the output of the AMMI model analysis, the genotypic main effect accounted for most of the total phenotypic variance in fresh root yield and some yield determining traits. This agreed with the findings of Tumuhimbise *et al.* (2014) on 12 cassava genotypes planted out in 3 contrasting environments. This is contrary to the findings of Daemo *et al.* (2023) who reported that genotype-by-environment interaction contributed 61.36% to the overall variation observed for this trait from observations made on 25 cassava genotypes planted in 6 contrasting environments and Jiwuba *et al.* (2020) who reported 43.8% contribution of GEI to fresh root yield on 58 cassava F_1 hybrids and their 2 parents planted in 6 environments. The disparity observed in these experiments could be explained by the level of genetic stability amongst the breeding populations, since 453 cassava accessions, planted in 5 contrasting environments were used for this experiment.

The GGE biplot analysis demonstrated considerable variation in the discriminating ability and representativeness of test environments (Figures 6.1–6.2). Environments with longer vectors from the biplot origin exhibited stronger discriminatory power, a pattern consistent with previous studies (Amelework *et al.*, 2023; Mbe *et al.*, 2024). This suggests that such environments are more effective in differentiating genotypic performance, which is essential for selecting superior genotypes. The varied and unpredictable performance patterns across environments for these traits underscore the complexity of G×E interactions in cassava, as previously reported by (Mbe *et al.*, 2024) in multi-environment trials.

The representativeness of test environments was further illustrated by the angular relationships between environments and the average environment axis (AEA). Environments IK19 and IK20 consistently formed smaller angles with the AEA, indicating their higher representativeness of the overall testing network. This aligns with the findings of (Filho *et al.*, 2024; Mbe *et al.*, 2024), who emphasized that representative environments minimize bias in genotype evaluation.

The polygon view of the GGE biplots (Figures 6.3–6.4) revealed distinct sectors, each corresponding to a potential mega-environment. Genotypes positioned at the polygon vertices exhibited extreme responses, indicating specific adaptations to certain environments. Notably,

IK19 consistently clustered with a distinct mega-environment across traits, suggesting its potential as a key testing site for cassava breeding programs targeting regional adaptation this aligns with the submissions of (Mbe *et al*., 2024).

The "which-won-where" pattern is particularly valuable for breeders, as it helps identify genotypes with superior performance in specific environments. The results of this study suggest that certain genotypes may be optimally suited for particular agroecological zones, reinforcing the need for decentralized breeding approaches to address regional variability.

The ranking of test environments relative to the "ideal environment" (Figures 6.5–6.6) identified MK21and IK19 as the most balanced environments in terms of discriminating ability and representativeness for fresh root yield and starch content respectively. This finding supports the recommendations by (Amelework *et al*., 2023; Filho *et al*., 2024; Mbe *et al*., 2024; Uchendu *et al*., 2022b), that ideal environments should be prioritized in breeding programs to enhance selection efficiency.

The evaluation of genotypes relative to the "ideal genotype" (Figures 6.7–6.8) identified several high-performing and stable accessions. For fresh root yield, genotypes G418, G159 and G234 exhibited both above-average performance and stability, making them promising candidates for varietal release. Similarly, G83, G424, and G215 were outstanding for starch content. These results align with the stability parameters proposed by (Aghogho *et al*., 2022; Amelework *et al*., 2023; Chipeta *et al*., 2017; Mbe *et al*., 2024; Uchendu *et al*., 2022b)

In the Finlay-Wilkinson model, sensitivity is a measure of significant differences in the regression slope of genotypes on the environmental mean. This means that the genotypes exhibited differential performance in their response to changes in the environments. Considering the differential response of the genotypes to changes in the environment mean which is a function of sensitivity, in this experiment, only four traits were observed to display sensitivity: dry matter content, number of lodged plants per plot, shoot weight and root weight. This is the direct opposite of the findings of Bakare *et al*. (2022) who observed sensitivity for other yield traits viz: fresh root yield, dry yield, top yield, and harvest index. These findings also deviate from the findings of Aghogho *et al*. (2023), who reported sensitivity for dry root yield. This implies that the sensitivity of genotypes to varying environments is a function of the level of genotypic variability obtainable in a population and the number and components of the test environments.

High broad sense heritability values were observed for starch content (0.83), dry matter content (0.84), plant height at 9 months after planting (0.86), and harvest index (0.89). These traits are all related to the quality of fresh cassava roots, plant architecture and biomass, which

are essential determinants of yield and economic value of the fresh cassava roots. Similarly, high values of broad sense heritability were reported for the following yield-determining traits: fresh root weight (0.77) and fresh root yield (0.78). Given the high estimates of broad sense heritability for these traits, there is significant potential for genetic improvement of these traits in cassava through selection. According to the classification criteria outlined by Johnson *et al.* (1955), which categorized genetic advance as a percentage of mean (GAM) values that were less than (10%) as low, between (10 – 20%) as moderate (10−20%) and more than (20%) as high, high GAM values were recorded for all the traits except form stem diameter (16.8%), dry matter content (13.86%) and angle of branching (19.65%) which had moderate values of GAM.

The combination of high broad-sense heritability estimates and moderate to high values of GAM recorded for these traits indicate that the trait would respond favourably to selection, thereby resulting into enhanced improvement. When selection pressure is imposed on the top 5% of the base population, it is possible to achieve significant gains of up to 46% for both fresh root weight and fresh root yield, while gain of about 39% could be achieved for harvest index. Likewise, moderate genetic gains of about 14% and 23% could be realized for dry matter content and starch content respectively. This will enhance the improvement of the productivity of fresh cassava roots for industrial processing and consumption.

6.5 Conclusions

The interaction between genotype and environment was critical to the performance of the cassava accessions in respect of yield and plant architecture traits across the 5 test environments. Based on the positive correlation between the test environments the test environments were reduced to two mega environments for important trait like fresh root yield (mega environment 1 - MK22 and KN23 and mega environment 2 - IK20, IK21 and ON22) and three mega environments for starch content (mega environment 1- MK22 and KN23, mega environment 2 - IK20 and IK 21 and mega environment 3 - ON22). This will ensure cost effectiveness in resource allocation without the loss of any valuable data. In terms of the mean performance and the stability of each genotype across the testing environments, genotypes G418 (TMS18F1414P0017), G159 (TMS18F1260P0060) and G234 (TMS18F1313P0053) were found to be widely adaptable and had stability for fresh root yield and genotypes G83 (TMS18F1096P0013), G424 (TMS18F1436P0049) and G215 (TMS18F1306P0127) for starch content. Out of these six genotypes, G424 (TMS18F1436P0049) and G83

(TMS18F1096P0013) had relatively high values for fresh root yield as well as starch content. They also have erect plant type that is suitable for mechanized cultivation. These genotypes emerged as early candidates for these traits. Their status could be validated through further observations at the advanced breeding stage.

CHAPTER SEVEN

7.0 CONCLUSIONS AND RECOMMENDATIONS

7.1 Conclusions

i. A total of 17 significant SNPs were identified through the genome-wide association analysis.

ii. These significant SNPs were found to be associated with plant architecture and yield traits in cassava. Only 13 of these significant SNPs were linked to putative candidate genes for seven traits.

iii. A total of 18 putative candidate genes were identified for the seven traits including angle of branching (4), plant type (4), overall plant appearance (2), level of branching (4), harvest index (3), and number of harvested plants (1).

iv. These candidate genes exhibit various functions in relation to plant architecture, adaptation, yield, plant growth, development, stress response, and starch metabolism.

v. Out of the 18 putative candidate genes identified in this study, one novel gene (Manes.01G077900) was discovered. This represents a significant contribution to knowledge.

vi. The results obtained from this research produced identical results to the prediction metrics that were reported in previous trials with respect to the consistency and accuracy of spectra (NIRS) data that were obtained using the SCiO sensor spectrometer.

vii. The results revealed that spectra data obtained using the SCiO sensor spectrometer could be reliably used in estimating starch and dry matter content in fresh cassava roots.

viii. The polynomial regression model showed similar prediction accuracy for fresh root yield across two environments at 3, 6, and 9 months after planting.

ix. The linear regression model used NDVI data to predict yield or plant architecture traits directly. Based on the accuracy of prediction, there exist significant disparity between NDVI data obtained from Mokwa and Onne trials.

x. The performance of cassava accessions in terms of yield and plant architecture traits across five test environments was influenced by the genotypes, environments and the interaction between genotypes and environments.

xi. The observed genotypic variation could be exploited for genetic gains, but the interaction between genotype and environment could complicate this.

7.2 Recommendations

i. The findings of this study would provide a gateway into the exploration of the genetic control of cassava plant architecture and yield. This research output will provide cassava breeders with the genetic and molecular leverage required to fast-track cassava improvement for yield, productivity, and adaptation for mechanized cultivation and industrial use. However, to fully comprehend the connection between the candidate genes and the phenotypes observed in the genome-wide association study, validation studies involving fine mapping and pathway analysis must be conducted.

ii. The SCiO sensor spectrometer data can reliably estimate starch and dry matter content in fresh cassava roots. However, a holistic exploration of all statistical metrics is necessary while choosing the best pre-treatment algorithm to avoid model bias.

iii. The findings from the prediction models developed from the NDVI data should be further validated on new cassava accessions and at different environments.

iv. The identified accessions G424 (TMS18F1436P0049) and G83 (TMS18F1096P0013) with erect plant type as wll as broad adaptability and stability for fresh root yield and starch have the inherent potential for rapid improvement for these traits and suitability for mechanized cultivation.

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APPENDICES

Table 3.1 | Details of the Cassava Accessions used for the experiment.

Accession ID	Pedigree	Entry Type
IITA-TMS-IBA000070	TMEB459/?	Check
IITA-TMS-IBA30572	58308/BRANCA DE SANTA CATARINA	Check
IITA-TMS-IBA980581	IITA-TMS-IBA980581	Check
IITA-TMS-IBA982101	IITA-TMS-IBA951181/71173	Check
NR130124	NR130124	Check
TMEB419	TMEB419	Check
TMS13F1160P0004	IITA-TMS-IBA993073/IITA-TMS-IBA051740	Test
TMS13F1307P0016	IITA-TMS-IBA030060/IITA-TMS-IBA010903	Test
TMS13F1343P0022	IITA-TMS-IBA970425/IITA-TMS-IBA930007	Test
TMS13F1343P0044	IITA-TMS-IBA970425/IITA-TMS-IBA930007	Test
TMS18F1001P0014	TMS15F1004P0001/TMS15F1159P0006	Test
TMS18F1001P0020	TMS15F1004P0001/TMS15F1159P0006	Test
TMS18F1003P0003	TMS15F1021P0002/TMS15F1132P0003	Test
TMS18F1003P0009	TMS15F1021P0002/TMS15F1132P0003	Test
TMS18F1003P0014	TMS15F1021P0002/TMS15F1132P0003	Test
TMS18F1004P0008	TMS15F1021P0002/TMS15F1153P0009	Test
TMS18F1005P0023	TMS15F1021P0002/TMS15F1156P0014	Test
TMS18F1007P0004	TMS15F1021P0002/TMS15F1310P0019	Test
TMS18F1007P0005	TMS15F1021P0002/TMS15F1310P0019	Test
TMS18F1010P0011	TMS15F1025P0001/TMS15F1305P0021	Test
TMS18F1016P0010	TMS15F1069P0007/TMS15F1398P0008	Test
TMS18F1018P0001	TMS15F1072P0005/TMS15F1367P0001	Test
TMS18F1019P0018	TMS15F1072P0005/TMS15F1398P0008	Test
TMS18F1020P0027	TMS15F1072P0006/TMS15F1326P0004	Test
TMS18F1024P0020	TMS15F1072P0012/TMS15F1398P0008	Test
TMS18F1025P0041	TMS15F1072P0031/TMS15F1156P0014	Test
TMS18F1026P0009	TMS15F1072P0031/TMS15F1196P0010	Test
TMS18F1028P0003	TMS15F1073P0005/TMS15F1153P0009	Test
TMS18F1028P0030	TMS15F1073P0005/TMS15F1153P0009	Test
TMS18F1038P0010	TMS15F1080P0004/TMS15F1153P0009	Test
TMS18F1038P0056	TMS15F1080P0004/TMS15F1153P0009	Test
TMS18F1038P0087	TMS15F1080P0004/TMS15F1153P0009	Test
TMS18F1040P0032	TMS15F1080P0004/TMS15F1318P0024	Test
TMS18F1040P0044	TMS15F1080P0004/TMS15F1318P0024	Test
TMS18F1040P0054	TMS15F1080P0004/TMS15F1318P0024	Test
TMS18F1041P0002	TMS15F1080P0007/TMS15F1305P0017	Test
TMS18F1041P0005	TMS15F1080P0007/TMS15F1305P0017	Test
TMS18F1042P0009	TMS15F1080P0007/TMS15F1367P0001	Test

Accession ID	Pedigree	Entry Type
TMS18F1044P0013	TMS15F1080P0012/TMS15F1159P0006	Test
TMS18F1047p0012	TMS15F1080P0012/TMS15F1398P0008	Test
TMS18F1047P0045	TMS15F1080P0012/TMS15F1398P0008	Test
TMS18F1047P0046	TMS15F1080P0012/TMS15F1398P0008	Test
TMS18F1047P0049	TMS15F1080P0012/TMS15F1398P0008	Test
TMS18F1048P0023	TMS15F1081P0003/TMS15F1072P0018	Test
TMS18F1051P0059	TMS15F1081P0003/TMS15F1156P0001	Test
TMS18F1051P0063	TMS15F1081P0003/TMS15F1156P0001	Test
TMS18F1055P0036	TMS15F1081P0003/TMS15F1367P0001	Test
TMS18F1055P0044	TMS15F1081P0003/TMS15F1367P0001	Test
TMS18F1056P0016	TMS15F1081P0003/TMS15F1398P0008	Test
TMS18F1056P0019	TMS15F1081P0003/TMS15F1398P0008	Test
TMS18F1056P0066	TMS15F1081P0003/TMS15F1398P0008	Test
TMS18F1058P0019	TMS15F1100P0005/TMS15F1132P0013	Test
TMS18F1058P0020	TMS15F1100P0005/TMS15F1132P0013	Test
TMS18F1059P0015	TMS15F1100P0005/TMS15F1153P0009	Test
TMS18F1060P0067	TMS15F1100P0005/TMS15F1156P0014	Test
TMS18F1063P0008	TMS15F1103P0006/TMS15F1153P0009	Test
TMS18F1064P0027	TMS15F1103P0006/TMS15F1156P0014	Test
TMS18F1065P0037	TMS15F1103P0006/TMS15F1195P0009	Test
TMS18F1068P0063	TMS15F1103P0006/TMS15F1305P0007	Test
TMS18F1068P0077	TMS15F1103P0006/TMS15F1305P0007	Test
TMS18F1069P0023	TMS15F1103P0006/TMS15F1318P0009	Test
TMS18F1069P0033	TMS15F1103P0006/TMS15F1318P0009	Test
TMS18F1073P0035	TMS15F1104P0001/TMS15F1156P0014	Test
TMS18F1073P0038	TMS15F1104P0001/TMS15F1156P0014	Test
TMS18F1076P0001	TMS15F1109P0003/TMS15F1156P0014	Test
TMS18F1076P0066	TMS15F1109P0003/TMS15F1156P0014	Test
TMS18F1076P0077	TMS15F1109P0003/TMS15F1156P0014	Test
TMS18F1076P0103	TMS15F1109P0003/TMS15F1156P0014	Test
TMS18F1076P0106	TMS15F1109P0003/TMS15F1156P0014	Test
TMS18F1076P0112	TMS15F1109P0003/TMS15F1156P0014	Test
TMS18F1076P0114	TMS15F1109P0003/TMS15F1156P0014	Test
TMS18F1076P0117	TMS15F1109P0003/TMS15F1156P0014	Test
TMS18F1076P0121	TMS15F1109P0003/TMS15F1156P0014	Test
TMS18F1081P0014	TMS15F1124P0001/TMS15F1214P0002	Test
TMS18F1082P0024	TMS15F1124P0001/TMS15F1351P0003	Test
TMS18F1083P0028	TMS15F1124P0001/TMS15F1367P0001	Test

Accession ID	Pedigree	Entry Type
TMS18F1085P0012	TMS15F1127P0002/TMS15F1156P0014	Test
TMS18F1090P0031	TMS15F1130P0012/TMS15F1153P0009	Test
TMS18F1092P0016	TMS15F1130P0012/TMS15F1396P0004	Test
TMS18F1096P0013	TMS15F1132P0001/TMS15F1177P0004	Test
TMS18F1096P0024	TMS15F1132P0001/TMS15F1177P0004	Test
TMS18F1107P0020	TMS15F1153P0009/TMS15F1177P0004	Test
TMS18F1113P0002	TMS15F1153P0009/TMS15F1396P0004	Test
TMS18F1113P0038	TMS15F1153P0009/TMS15F1396P0004	Test
TMS18F1114P0039	TMS15F1153P0009/TMS15F1397P0001	Test
TMS18F1120P0004	TMS15F1154P0002/TMS15F1196P0010	Test
TMS18F1120P0006	TMS15F1154P0002/TMS15F1196P0010	Test
TMS18F1121P0029	TMS15F1154P0002/TMS15F1318P0024	Test
TMS18F1127P0011	TMS15F1154P0015/TMS15F1396P0007	Test
TMS18F1127P0010	TMS15F1154P0015/TMS15F1396P0007	Test
TMS18F1132P0042	TMS15F1156P0006/TMS15F1196P0010	Test
TMS18F1132P0078	TMS15F1156P0006/TMS15F1196P0010	Test
TMS18F1132P0083	TMS15F1156P0006/TMS15F1196P0010	Test
TMS18F1132P0144	TMS15F1156P0006/TMS15F1196P0010	Test
TMS18F1134P0010	TMS15F1156P0014/TMS15F1318P0024	Test
TMS18F1135P0025	TMS15F1072P0005/TMS15F1326P0004	Test
TMS18F1138P0028	TMS15F1160P0010/TMS15F1284P0008	Test
TMS18F1138P0030	TMS15F1160P0010/TMS15F1284P0008	Test
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TMS18F1138P0037	TMS15F1160P0010/TMS15F1284P0008	Test
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TMS18F1142P0017	TMS15F1160P0010/TMS15F1396P0004	Test
TMS18F1144P0010	TMS15F1195P0006/TMS15F1310P0019	Test
TMS18F1149P0024	TMS15F1196P0010/TMS15F1310P0019	Test
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TMS18F1153P0053	TMS15F1230P0005/TMS15F1132P0001	Test
TMS18F1156P0016	TMS15F1230P0005/TMS15F1300P0002	Test
TMS18F1163P0035	TMS15F1244P0004/TMS15F1132P0013	Test
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TMS18F1165P0008	TMS15F1269P0004/TMS15F1318P0009	Test
TMS18F1165P0018	TMS15F1269P0004/TMS15F1318P0009	Test
TMS18F1174P0011	TMS15F1270P0001/TMS15F1328P0001	Test

Accession ID	Pedigree	Entry Type
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TMS18F1179P0008	TMS15F1276P0003/TMS15F1318P0009	Test
TMS18F1179P0029	TMS15F1276P0003/TMS15F1318P0009	Test
TMS18F1180P0033	TMS15F1295P0001/TMS15F1321P0001	Test
TMS18F1191P0002	TMS15F1305P0021/TMS15F1201P0017	Test
TMS18F1202p0001	TMS15F1321P0001/TMS15F1024P0006	Test
TMS18F1205P0010	TMS15F1321P0003/TMS15F1367P0001	Test
TMS18F1207P0008	TMS15F1324P0004/TMS15F1159P0001	Test
TMS18F1208P0005	TMS15F1300P0002/TMS15F1072P0012	Test
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TMS18F1209P0015	TMS15F1326P0004/TMS15F1159P0001	Test
TMS18F1210P0021	TMS15F1326P0004/TMS15F1367P0001	Test
TMS18F1211P0035	TMS15F1328P0001/TMS15F1069P0007	Test
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TMS18F1217P0034	TMS15F1351P0003/TMS15F1069P0007	Test
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TMS18F1217P0095	TMS15F1351P0003/TMS15F1069P0007	Test
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TMS18F1222P0012	TMS15F1367P0001/TMS15F1132P0001	Test
TMS18F1224P0014	TMS15F1310P0019/TMS15F1156P0014	Test
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TMS18F1250P0050	TMS15F1424P0004/TMS15F1195P0006	Test
TMS18F1258P0062	TMS13F1020P0001/IITA-TMS-IBA930007	Test
TMS18F1258P0147	TMS13F1020P0001/IITA-TMS-IBA930007	Test
TMS18F1258P0153	TMS13F1020P0001/IITA-TMS-IBA930007	Test
TMS18F1258P0156	TMS13F1020P0001/IITA-TMS-IBA930007	Test
TMS18F1259P0131	TMS13F1020P0001/IITA-TMS-IBA972205	Test
TMS18F1260P0054	TMS13F1020P0001/TMEB419	Test

Accession ID	Pedigree	Entry Type
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TMS18F1261P0005	TMS13F1020P0001/TMS13F1088P0007	Test
TMS18F1262P0008	TMS13F1020P0001/TMS13F1122P0005	Test
TMS18F1262P0015	TMS13F1020P0001/TMS13F1122P0005	Test
TMS18F1263P0037	TMS13F1053P0010/IITA-TMS-IBA000070	Test
TMS18F1264P0058	TMS13F1053P0010/IITA-TMS-IBA030060A	Test
TMS18F1265P0030	TMS13F1053P0010/IITA-TMS-IBA030060	Test
TMS18F1271P0001	TMS13F1053P0010/TMS13F1227P0143	Test
TMS18F1272P0037	TMS13F1053P0010/TMS13F1307P0016	Test
TMS18F1274P0020	TMS13F1053P0010/TMS13F1343P0022	Test
TMS18F1277P0007	TMS13F1053P0015/IITA-TMS-IBA930007	Test
TMS18F1277P0031	TMS13F1053P0015/IITA-TMS-IBA930007	Test
TMS18F1277P0045	TMS13F1053P0015/IITA-TMS-IBA930007	Test
TMS18F1278P0068	TMS13F1053P0015/IITA-TMS-IBA972205	Test
TMS18F1278P0098	TMS13F1053P0015/IITA-TMS-IBA972205	Test
TMS18F1278P0118	TMS13F1053P0015/IITA-TMS-IBA972205	Test
TMS18F1278P0165	TMS13F1053P0015/IITA-TMS-IBA972205	Test
TMS18F1278P0183	TMS13F1053P0015/IITA-TMS-IBA972205	Test
TMS18F1280P0057	TMS13F1053P0015/TMS13F1088P0007	Test
TMS18F1280P0086	TMS13F1053P0015/TMS13F1088P0007	Test
TMS18F1280P0091	TMS13F1053P0015/TMS13F1088P0007	Test
TMS18F1280P0107	TMS13F1053P0015/TMS13F1088P0007	Test
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TMS18F1280P0140	TMS13F1053P0015/TMS13F1088P0007	Test
TMS18F1280P0151	TMS13F1053P0015/TMS13F1088P0007	Test
TMS18F1282P0049	TMS13F1063P0013/IITA-TMS-IBA930007	Test
TMS18F1284P0003	TMS13F1063P0013/TMEB419	Test
TMS18F1286P0012	TMS13F1088P0007/IITA-TMS-IBA972205	Test
TMS18F1287P0029	TMS13F1088P0007/TMS13F1343P0002	Test
TMS18F1287P0039	TMS13F1088P0007/TMS13F1343P0002	Test
TMS18F1289P0014	TMS13F1106P0004/TMS13F1088P0007	Test
TMS18F1291P0014	TMS13F1122P0005/IITA-TMS-IBA972205	Test
TMS18F1291P0026	TMS13F1122P0005/IITA-TMS-IBA972205	Test
TMS18F1295P0023	TMS13F1160P0005/TMEB419	Test
TMS18F1295P0034	TMS13F1160P0005/TMEB419	Test
TMS18F1295P0035	TMS13F1160P0005/TMEB419	Test

Accession ID	Pedigree	Entry Type
TMS18F1296P0042	TMS13F1160P0005/TMS14F1284P0001	Test
TMS18F1296P0071	TMS13F1160P0005/TMS14F1284P0001	Test
TMS18F1298P0017	TMS13F1284P0001/IITA-TMS-IBA000070	Test
TMS18F1298P0044	TMS13F1284P0001/IITA-TMS-IBA000070	Test
TMS18F1299P0005	TMS13F1284P0001/TMEB419	Test
TMS18F1302P0018	TMS13F1307P0016/IITA-TMS-IBA000070	Test
TMS18F1303P0027	TMS13F1307P0016/IITA-TMS-IBA030060	Test
TMS18F1305P0007	TMS13F1307P0016/IITA-TMS-IBA930007	Test
TMS18F1305P0017	TMS13F1307P0016/IITA-TMS-IBA930007	Test
TMS18F1305P0019	TMS13F1307P0016/IITA-TMS-IBA930007	Test
TMS18F1305P0031	TMS13F1307P0016/IITA-TMS-IBA930007	Test
TMS18F1305P0039	TMS13F1307P0016/IITA-TMS-IBA930007	Test
TMS18F1305P0040	TMS13F1307P0016/IITA-TMS-IBA930007	Test
TMS18F1305P0138	TMS13F1307P0016/IITA-TMS-IBA930007	Test
TMS18F1306P0114	TMS13F1307P0016/IITA-TMS-IBA972205	Test
TMS18F1306P0127	TMS13F1307P0016/IITA-TMS-IBA972205	Test
TMS18F1306P0129	TMS13F1307P0016/IITA-TMS-IBA972205	Test
TMS18F1306P0135	TMS13F1307P0016/IITA-TMS-IBA972205	Test
TMS18F1306P0149	TMS13F1307P0016/IITA-TMS-IBA972205	Test
TMS18F1307P0001	TMS13F1307P0016/TMEB419	Test
TMS18F1308P0077	TMS13F1307P0016/TMS13F1053P0015	Test
TMS18F1308P0082	TMS13F1307P0016/TMS13F1053P0015	Test
TMS18F1308P0084	TMS13F1307P0016/TMS13F1053P0015	Test
TMS18F1308P0114	TMS13F1307P0016/TMS13F1053P0015	Test
TMS18F1309P0062	TMS13F1307P0016/TMS13F1069P0024	Test
TMS18F1309P0074	TMS13F1307P0016/TMS13F1069P0024	Test
TMS18F1310P0088	TMS13F1307P0016/TMS13F1088P0007	Test
TMS18F1310P0148	TMS13F1307P0016/TMS13F1088P0007	Test
TMS18F1310P0151	TMS13F1307P0016/TMS13F1088P0007	Test
TMS18F1310P0168	TMS13F1307P0016/TMS13F1088P0007	Test
TMS18F1312P0033	TMS13F1307P0016/TMS13F1227P0143	Test
TMS18F1312P0039	TMS13F1307P0016/TMS13F1227P0143	Test
TMS18F1313P0001	TMS13F1307P0016/TMS13F1343P0002	Test
TMS18F1313P0013	TMS13F1307P0016/TMS13F1343P0002	Test
TMS18F1313P0053	TMS13F1307P0016/TMS13F1343P0002	Test
TMS18F1314P0007	TMS13F1307P0016/TMS13F1343P0022	Test
TMS18F1314P0026	TMS13F1307P0016/TMS13F1343P0022	Test
TMS18F1314P0042	TMS13F1307P0016/TMS13F1343P0022	Test

Accession ID	Pedigree	Entry Type
TMS18F1317P0048	TMS13F1343P0002/IITA-TMS-IBA030060A	Test
TMS18F1317P0059	TMS13F1343P0002/IITA-TMS-IBA030060A	Test
TMS18F1317P0119	TMS13F1343P0002/IITA-TMS-IBA030060A	Test
TMS18F1317P0123	TMS13F1343P0002/IITA-TMS-IBA030060A	Test
TMS18F1318P0007	TMS13F1343P0002/IITA-TMS-IBA930007	Test
TMS18F1318P0016	TMS13F1343P0002/IITA-TMS-IBA930007	Test
TMS18F1318P0018	TMS13F1343P0002/IITA-TMS-IBA930007	Test
TMS18F1318P0036	TMS13F1343P0002/IITA-TMS-IBA930007	Test
TMS18F1318P0054	TMS13F1343P0002/IITA-TMS-IBA930007	Test
TMS18F1319P0033	TMS13F1343P0002/IITA-TMS-IBA972205	Test
TMS18F1319P0061	TMS13F1343P0002/IITA-TMS-IBA972205	Test
TMS18F1319P0100	TMS13F1343P0002/IITA-TMS-IBA972205	Test
TMS18F1319P0121	TMS13F1343P0002/IITA-TMS-IBA972205	Test
TMS18F1319P0159	TMS13F1343P0002/IITA-TMS-IBA972205	Test
TMS18F1320P0032	TMS13F1343P0002/TMEB419	Test
TMS18F1320P0051	TMS13F1343P0002/TMEB419	Test
TMS18F1320P0082	TMS13F1343P0002/TMEB419	Test
TMS18F1320P0086	TMS13F1343P0002/TMEB419	Test
TMS18F1320P0087	TMS13F1343P0002/TMEB419	Test
TMS18F1320P0101	TMS13F1343P0002/TMEB419	Test
TMS18F1322P0019	TMS13F1343P0002/TMS13F1343P0022	Test
TMS18F1323P0002	TMS13F1343P0022/IITA-TMS-IBA930007	Test
TMS18F1323P0024	TMS13F1343P0022/IITA-TMS-IBA930007	Test
TMS18F1323P0041	TMS13F1343P0022/IITA-TMS-IBA930007	Test
TMS18F1323p0025	TMS13F1343P0022/IITA-TMS-IBA930007	Test
TMS18F1324P0003	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1324P0046	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1324P0070	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1324P0089	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1324P0092	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1324P0093	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1324P0107	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1324P0171	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1324P0200	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1324p0026	TMS13F1343P0022/IITA-TMS-IBA972205	Test
TMS18F1325P0032	TMS13F1343P0022/TMEB419	Test
TMS18F1326P0007	TMS13F1343P0022/TMS13F1053P0015	Test
TMS18F1327P0006	TMS13F1343P0022/TMS13F1069P0024	Test

Accession ID	Pedigree	Entry Type
TMS18F1327P0013	TMS13F1343P0022/TMS13F1069P0024	Test
TMS18F1328P0027	TMS13F1343P0022/TMS13F1088P0007	Test
TMS18F1328P0032	TMS13F1343P0022/TMS13F1088P0007	Test
TMS18F1329P0011	TMS13F1343P0022/TMS13F1122P0005	Test
TMS18F1330P0008	TMS13F1343P0038/TMEB419	Test
TMS18F1330P0009	TMS13F1343P0038/TMEB419	Test
TMS18F1330P0020	TMS13F1343P0038/TMEB419	Test
TMS18F1331P0013	TMS13F1362P0004/IITA-TMS-IBA000070	Test
TMS18F1331P0016	TMS13F1362P0004/IITA-TMS-IBA000070	Test
TMS18F1332P0002	TMS13F1362P0004/TMEB419	Test
TMS18F1333P0012	TMS13F1362P0004/TMS13F1343P0038	Test
TMS18F1333p0013	TMS13F1362P0004/TMS13F1343P0038	Test
TMS18F1334P0003	TMS13F1377P0018/IITA-TMS-IBA000070	Test
TMS18F1334P0023	TMS13F1377P0018/IITA-TMS-IBA000070	Test
TMS18F1335P0001	TMS13F1377P0018/IITA-TMS-IBA030060	Test
TMS18F1335P0021	TMS13F1377P0018/IITA-TMS-IBA030060	Test
TMS18F1335P0035	TMS13F1377P0018/IITA-TMS-IBA030060	Test
TMS18F1336P0014	TMS13F1377P0018/IITA-TMS-IBA030060A	Test
TMS18F1336P0015	TMS13F1377P0018/IITA-TMS-IBA030060A	Test
TMS18F1337P0044	TMS13F1377P0018/IITA-TMS-IBA930007	Test
TMS18F1337P0049	TMS13F1377P0018/IITA-TMS-IBA930007	Test
TMS18F1338P0013	TMS13F1377P0018/IITA-TMS-IBA972205	Test
TMS18F1338P0053	TMS13F1377P0018/IITA-TMS-IBA972205	Test
TMS18F1338P0067	TMS13F1377P0018/IITA-TMS-IBA972205	Test
TMS18F1338P0085	TMS13F1377P0018/IITA-TMS-IBA972205	Test
TMS18F1338P0099	TMS13F1377P0018/IITA-TMS-IBA972205	Test
TMS18F1338P0115	TMS13F1377P0018/IITA-TMS-IBA972205	Test
TMS18F1338P0116	TMS13F1377P0018/IITA-TMS-IBA972205	Test
TMS18F1339P0012	TMS13F1377P0018/TMEB419	Test
TMS18F1339P0015	TMS13F1377P0018/TMEB419	Test
TMS18F1340P0001	TMS13F1377P0018/TMS13F1069P0024	Test
TMS18F1340P0030	TMS13F1377P0018/TMS13F1069P0024	Test
TMS18F1341P0037	TMS13F1377P0018/TMS13F1122P0005	Test
TMS18F1341P0044	TMS13F1377P0018/TMS13F1122P0005	Test
TMS18F1342P0003	TMS13F1377P0018/TMS13F1343P0002	Test
TMS18F1342P0017	TMS13F1377P0018/TMS13F1343P0002	Test
TMS18F1343P0012	TMS13F1053P0010/IITA-TMS-IBA930007	Test
TMS18F1343P0014	TMS13F1053P0010/IITA-TMS-IBA930007	Test

Accession ID	Pedigree	Entry Type
TMS18F1343P0064	TMS13F1053P0010/IITA-TMS-IBA930007	Test
TMS18F1343P0153	TMS13F1053P0010/IITA-TMS-IBA930007	Test
TMS18F1343P0171	TMS13F1053P0010/IITA-TMS-IBA930007	Test
TMS18F1344P0003	TMS13F1053P0010/IITA-TMS-IBA972205	Test
TMS18F1344P0014	TMS13F1053P0010/IITA-TMS-IBA972205	Test
TMS18F1344P0100	TMS13F1053P0010/IITA-TMS-IBA972205	Test
TMS18F1344P0133	TMS13F1053P0010/IITA-TMS-IBA972205	Test
TMS18F1344P0147	TMS13F1053P0010/IITA-TMS-IBA972205	Test
TMS18F1344P0153	TMS13F1053P0010/IITA-TMS-IBA972205	Test
TMS18F1344P0159	TMS13F1053P0010/IITA-TMS-IBA972205	Test
TMS18F1344P0176	TMS13F1053P0010/IITA-TMS-IBA972205	Test
TMS18F1344P0198	TMS13F1053P0010/IITA-TMS-IBA972205	Test
TMS18F1345P0001	TMS13F1053P0010/TMEB419	Test
TMS18F1345P0012	TMS13F1053P0010/TMEB419	Test
TMS18F1345P0043	TMS13F1053P0010/TMEB419	Test
TMS18F1345P0056	TMS13F1053P0010/TMEB419	Test
TMS18F1346P0023	TMS13F1063P0013/TMS13F1343P0002	Test
TMS18F1347P0029	TMS13F1088P0007/IITA-TMS-IBA030060A	Test
TMS18F1348P0024	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348p0039	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0051	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0088	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0092	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0095	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0097	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0098	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0101	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0113	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0117	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0131	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0156	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1348P0157	TMS13F1088P0007/IITA-TMS-IBA930007	Test
TMS18F1349P0064	TMS13F1088P0007/IITA-TMS-IBA972205	Test
TMS18F1349P0065	TMS13F1088P0007/IITA-TMS-IBA972205	Test
TMS18F1349P0123	TMS13F1088P0007/IITA-TMS-IBA972205	Test
TMS18F1349P0126	TMS13F1088P0007/IITA-TMS-IBA972205	Test
TMS18F1349P0149	TMS13F1088P0007/IITA-TMS-IBA972205	Test
TMS18F1349P0157	TMS13F1088P0007/IITA-TMS-IBA972205	Test

Accession ID	Pedigree	Entry Type
TMS18F1350P0026	TMS13F1088P0007/TMEB419	Test
TMS18F1350P0038	TMS13F1088P0007/TMEB419	Test
TMS18F1350P0041	TMS13F1088P0007/TMEB419	Test
TMS18F1350P0056	TMS13F1088P0007/TMEB419	Test
TMS18F1350P0065	TMS13F1088P0007/TMEB419	Test
TMS18F1350P0082	TMS13F1088P0007/TMEB419	Test
TMS18F1350P0091	TMS13F1088P0007/TMEB419	Test
TMS18F1352P0002	TMS13F1160P0005/IITA-TMS-IBA000070	Test
TMS18F1352P0016	TMS13F1160P0005/IITA-TMS-IBA000070	Test
TMS18F1352P0049	TMS13F1160P0005/IITA-TMS-IBA000070	Test
TMS18F1353p0017	TMS13F1106P0004/TMS13F1122P0005	Test
TMS18F1353P0022	TMS13F1106P0004/TMS13F1122P0005	Test
TMS18F1353P0023	TMS13F1106P0004/TMS13F1122P0005	Test
TMS18F1353P0038	TMS13F1106P0004/TMS13F1122P0005	Test
TMS18F1354P0027	TMS13F1343P0022/IITA-TMS-IBA000070	Test
TMS18F1355p0025	TMS13F1343P0022/IITA-TMS-IBA030060A	Test
TMS18F1355P0081	TMS13F1343P0022/IITA-TMS-IBA030060A	Test
TMS18F1355P0089	TMS13F1343P0022/IITA-TMS-IBA030060A	Test
TMS18F1355P0120	TMS13F1343P0022/IITA-TMS-IBA030060A	Test
TMS18F1355p0038	TMS13F1343P0022/IITA-TMS-IBA030060A	Test
TMS18F1359P0001	TMS14F1201P0003/TMS14F1284P0001	Test
TMS18F1361P0018	TMS15F1041P0003/TMS15F1021P0028	Test
TMS18F1361P0041	TMS15F1041P0003/TMS15F1021P0028	Test
TMS18F1364P0018	TMS15F1143P0004/IITA-TMS-IKN130010	Test
TMS18F1364P0022	TMS15F1143P0004/IITA-TMS-IKN130010	Test
TMS18F1364P0027	TMS15F1143P0004/IITA-TMS-IKN130010	Test
TMS18F1365P0005	TMS15F1159P0006/IITA-TMS-IKN130010	Test
TMS18F1365P0018	TMS15F1159P0006/IITA-TMS-IKN130010	Test
TMS18F1365P0022	TMS15F1159P0006/IITA-TMS-IKN130010	Test
TMS18F1365P0024	TMS15F1159P0006/IITA-TMS-IKN130010	Test
TMS18F1366P0012	TMS15F1159P0006/TMS15F1021P0028	Test
TMS18F1366P0014	TMS15F1159P0006/TMS15F1021P0028	Test
TMS18F1367P0030	TMS15F1159P0006/TMS15F1305P0017	Test
TMS18F1369P0014	TMS15F1305P0017/TMS15F1021P0028	Test
TMS18F1369P0015	TMS15F1305P0017/TMS15F1021P0028	Test
TMS18F1369P0023	TMS15F1305P0017/TMS15F1021P0028	Test
TMS18F1370P0008	TMS15F1318P0009/TMS15F1041P0003	Test
TMS18F1371P0001	TMS15F1318P0009/TMS15F1305P0007	Test

Accession ID	Pedigree	Entry Type
TMS18F1371P0011	TMS15F1318P0009/TMS15F1305P0007	Test
TMS18F1372P0024	TMS15F1329P0005/TMS15F1021P0028	Test
TMS18F1372P0041	TMS15F1329P0005/TMS15F1021P0028	Test
TMS18F1373P0028	TMS15F1329P0005/TMS15F1041P0003	Test
TMS18F1377P0007	TMS15F1396P0001/TMS15F1296P0001	Test
TMS18F1377P0023	TMS15F1396P0001/TMS15F1296P0001	Test
TMS18F1380P0003	IITA-TMS-IBA011368/IITA-TMS-IKN130010	Test
TMS18F1388P0012	IITA-TMS-IBA070337/IITA-TMS-IBA141092	Test
TMS18F1389P0021	IITA-TMS-IBA070337/TMS14F1319P0004	Test
TMS18F1389P0031	IITA-TMS-IBA070337/TMS14F1319P0004	Test
TMS18F1391P0004	IITA-TMS-IBA070593/IITA-TMS-IBA011797	Test
TMS18F1395P0010	IITA-TMS-IBA070593/IITA-TMS-IBA930007	Test
TMS18F1395P0038	IITA-TMS-IBA070593/IITA-TMS-IBA930007	Test
TMS18F1395P0055	IITA-TMS-IBA070593/IITA-TMS-IBA930007	Test
TMS18F1396P0017	IITA-TMS-IBA070593/IITA-TMS-IBA972205	Test
TMS18F1396P0053	IITA-TMS-IBA070593/IITA-TMS-IBA972205	Test
TMS18F1408P0006	IITA-TMS-IBA011797/IITA-TMS-IBA030060A	Test
TMS18F1409P0008	IITA-TMS-IBA011797/IITA-TMS-IBA972205	Test
TMS18F1414P0014	IITA-TMS-IBA070337/IITA-TMS-IBA972205	Test
TMS18F1414P0017	IITA-TMS-IBA070337/IITA-TMS-IBA972205	Test
TMS18F1421P0005	IITA-TMS-IBA090516/IITA-TMS-IKN120210	Test
TMS18F1421P0025	IITA-TMS-IBA090516/IITA-TMS-IKN120210	Test
TMS18F1424P0021	IITA-TMS-IBA090516/TMEB693	Test
TMS18F1426P0001	IITA-TMS-IBA141092/IITA-TMS-IBA30572	Test
TMS18F1436P0049	IITA-TMS-IBA141092/1629MP2	Test
TMS18F1436P0053	IITA-TMS-IBA141092/1629MP2	Test
TMS18F1447P0002	IITA-TMS-IBA30572/IITA-TMS-IBA011368	Test
TMS18F1447P0045	IITA-TMS-IBA30572/IITA-TMS-IBA011368	Test
TMS18F1447P0062	IITA-TMS-IBA30572/IITA-TMS-IBA011368	Test
TMS18F1447P0078	IITA-TMS-IBA30572/IITA-TMS-IBA011368	Test
TMS18F1469P0062	TMEB419/TMS14F1319P0004	Test
TMS18F1472P0042	TMEB693/IITA-TMS-IBA030060	Test
TMS18F1476P0047	TMEB693/IITA-TMS-IKN130010	Test
TMS18F1478P0047	TMEB693/TMS13F1475P0217	Test
TMS18F1480P0023	TMEB693/TMS14F1234P0001	Test
TMS18F1481P0009	TMS13F1053P0010/IITA-TMS-IBA030060A	Test
TMS18F1481P0015	TMS13F1053P0010/IITA-TMS-IBA030060A	Test
TMS18F1484P0036	TMS13F1053P0010/IITA-TMS-IBA141092	Test

Accession ID	Pedigree	Entry Type
TMS18F1485P0022	TMS14F1284P0001/TMS13F1227P0119	Test
TMS18F1489P0038	TMS13F1088P0007/TMS13F1343P0002	Test
TMS18F1489P0044	TMS13F1088P0007/TMS13F1343P0002	Test
TMS18F1489P0040	TMS13F1088P0007/TMS13F1343P0002	Test
TMS18F1505P0047	TMS13F1307P0016/IITA-TMS-IBA930007	Test
TMS18F1505P0057	TMS13F1307P0016/IITA-TMS-IBA930007	Test
TMS18F1506P0018	TMS13F1307P0016/IITA-TMS-IBA972205	Test
TMS18F1520P0039	TMS14F1201P0003/TMEB419	Test
TMS18F1520P0050	TMS14F1201P0003/TMEB419	Test
TMS18F1539P0063	TMEB419/TMS14F1073P0001	Test
TMS18F1539P0073	TMEB419/TMS14F1073P0001	Test
TMS18F1562P0023	IITA-TMS-IBA071313/IITA-TMS-IBA930007	Test
TMS18F1562P0025	IITA-TMS-IBA071313/IITA-TMS-IBA930007	Test
TMS18F1562P0026	IITA-TMS-IBA071313/IITA-TMS-IBA930007	Test
TMS18F1562P0030	IITA-TMS-IBA071313/IITA-TMS-IBA930007	Test
TMS18F1562P0055	IITA-TMS-IBA071313/IITA-TMS-IBA930007	Test

Table 3.2| description of the five commercial check varieties used for this research

Variety	Yield (t/ha)	Dry Matter Content (%)	Starch Content (%)	Physiology	Other Features
TMEB419 (TME419)	36	40		Erect, straight type excellent for mechanization	Green petiole, light brown stem, light/cream root, CMD resistance, low cyanide potential, Good for starch, flour, garri, and fresh consumption
IITA-TMS-IBA000070 (BABA-70)	37.5	38.5	28	Compact plant type, light brown stem, and red petiole color	High yielding and early bulking, good weed control, moderate dry matter content, resistant to Cassava Mosaic Disease (CMD), excellent for gari and fufu
IITA-TMS-IBA98058 (Dixon)	35	35		Erect plant type, excellent drought tolerance	Red petiole, silver-green stem, white root, CMD and CGM resistant, drought tolerant, Good for garri production
NR130124 (HOPE)	40.1	33.2	24.3	Compact branching pattern	Resistant to Cassava Mosaic Disease (CMD), cassava anthracnose disease (CAD), cassava mealybug (CM), cassava bacterial blight (CBB), and cassava green mite (CGM). Good for mechanization and has high fresh root yield, Excellent for gari and fufu production
IITA-TMS-IBA30572	>25	25		Compact structure with good branching habits	Moderate CMD resistance, early bulking, high starch and high yielding
IITA-TMS-IBA982101	>25	32		Compact structure with good branching habits	

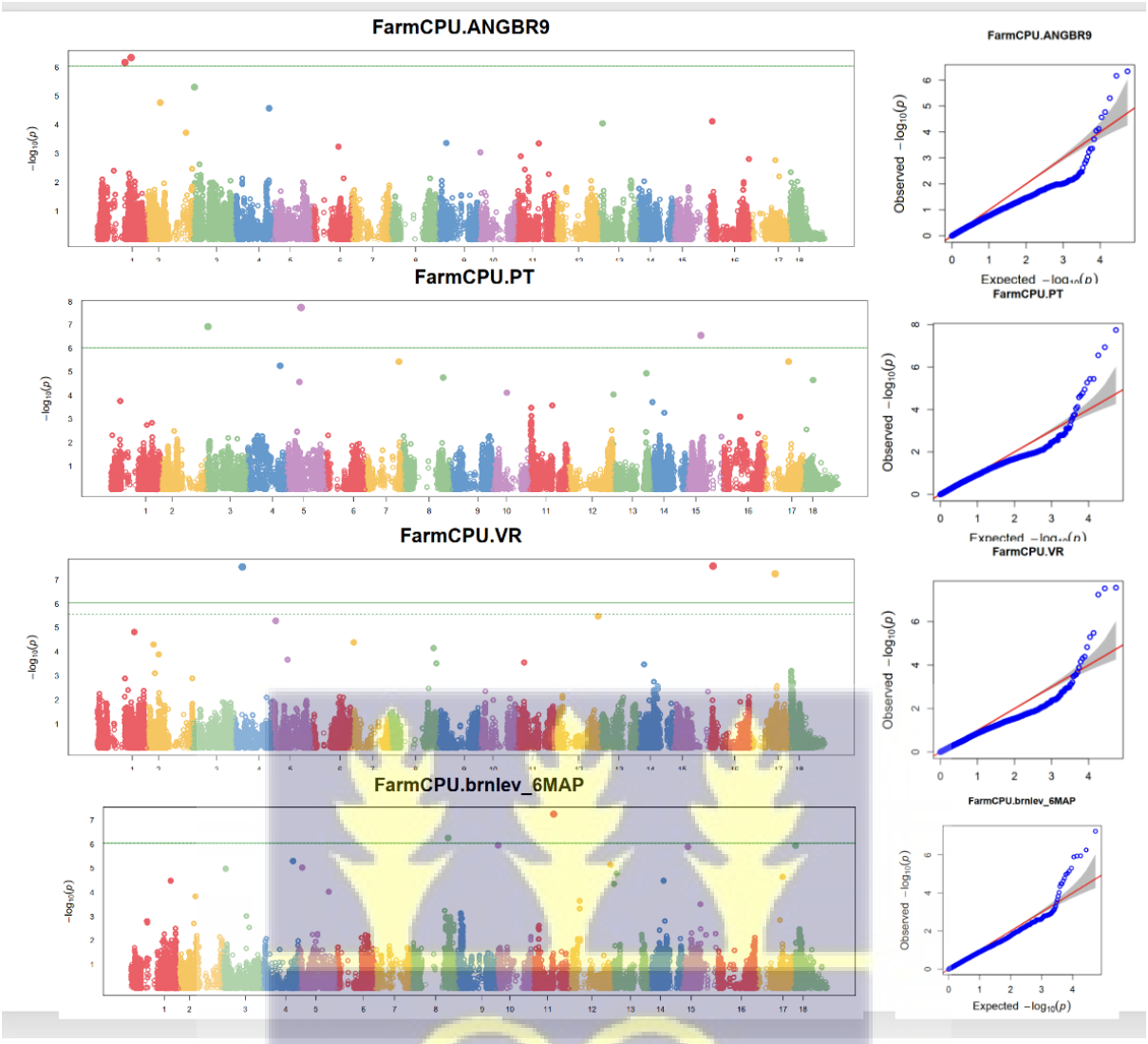
Source: (BASICS-II, 2020; Cassava Seed Tracker, 2019)

Table 3.3 | Plant Architecture Traits and their mode of scoring

Traits	Mode of Scoring
Stem diameter (STMDI9) (mm)	Measured using digital vernier caliper
Shoot weight (SHTWT) (kg)	Total weight of aboveground biomass (stems and leaves) per plot at harvest
Plant height at 9 months after planting (PLTHT9) (cm)	Measured using meter rule
Number of lodged plants per plot (LODG)	Count
Branching habit at 9 months after planting (BRNHB9)	Categorical Scoring
Angle of branching (ANGBR9) (0)	Measured using digital compass
Number of plants per stand (PPSTD9)	Count
Height at first branch at 9 months after planting (BRNHT9) (cm)	Measured using meter rule
Plant height at 6 months after planting (PLTHT6) (cm)	Measured using meter rule
Top yield (TYLD) (t/ha)	Estimate: (SHTWT/(MaxNumberHarvested) * 12000/1000)
Height at first branch at 6 months after planting (BRNHT6) (cm)	Measured using meter rule

Table 3.4 | Yield-Related Traits and their mode of scoring

Traits	Mode of Scoring
Fresh root yield (FYLD) (t/ha)	Estimate: (RTWT/(MaxNumberHarvested) * 12000/1000)
Dry yield (DYLD) (t/ha)	Estimate (FYLD*(DM/100))
Starch content (SC) (%)	Estimate: Specific gravity (SG) method (210.8 * SG -213.4)
Dry matter content (DM) (%)	Estimate: Specific gravity (SG) method (158.3 * SG -142)
Number of harvested roots (RTNO)	Count
Fresh root weight (RTWT) (kg)	Total weight of fresh roots harvested per plot at harvest
Harvest index (HI)	Estimate (Roots weight / Roots weight + Shoot weight)



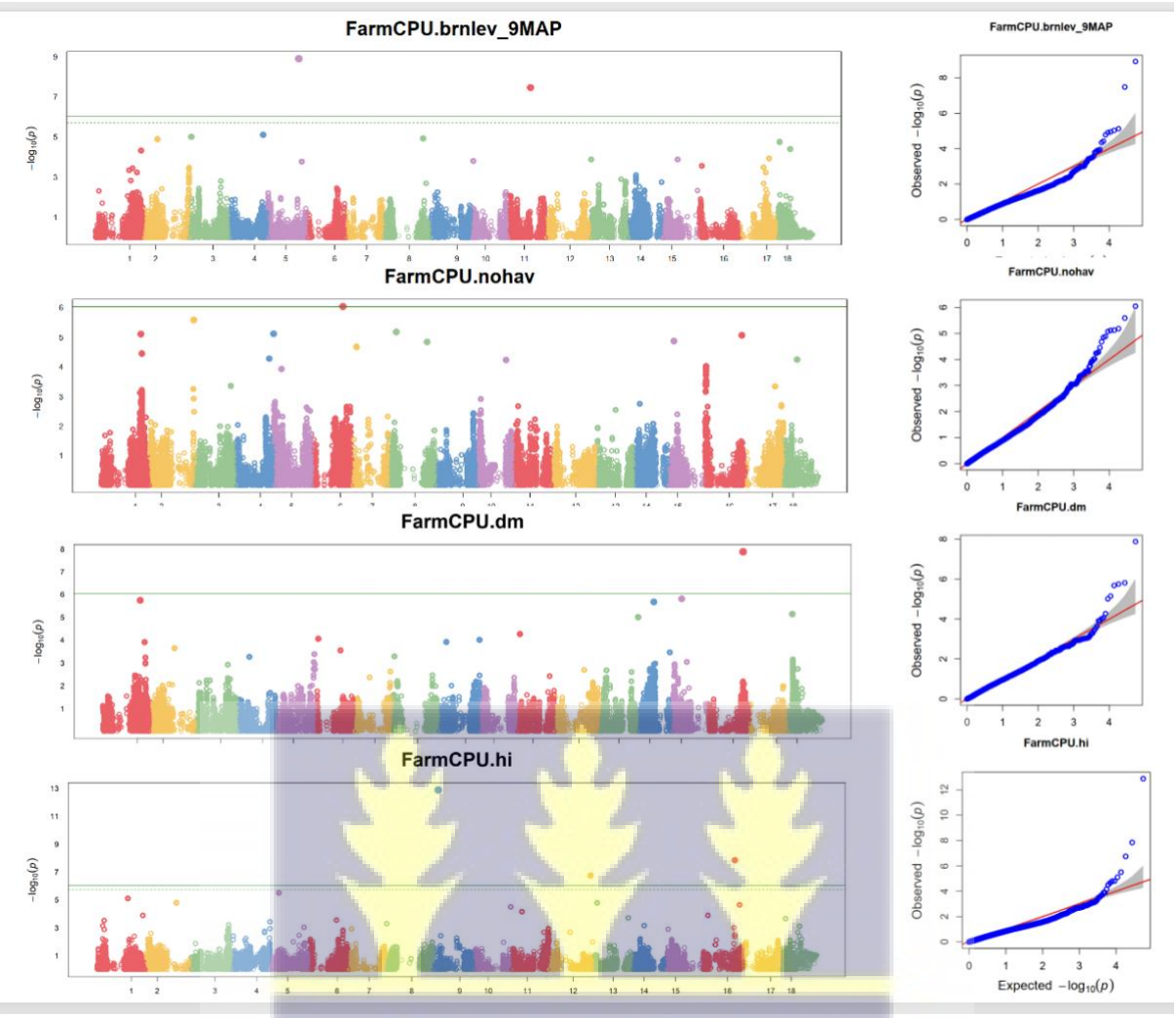


Figure 3.1 | Manhattan and QQ Plots of Significant SNPs