CHARACTERISATION OF UNDERUTILISED LEGUMES FOR CLIMATE-SMART AGRICULTURE UNDER WATER STRESS

BY

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Submitted in fulfilment of the academic requirements of

Doctor of Philosophy

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UNIVERSITY OF KWAZULU-NATAL

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2025

PREFACE

The research contained in this thesis was completed by the candidate while based in the Discipline of Crop Science, School of Agricultural, Earth and Environmental Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, South Africa. The research was financially supported by National Research Foundation.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

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DECLARATION 1: PLAGIARISM

I, Anne Chisa, declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;

(iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

(iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a) their words have been re-written but the general information attributed to them has been referenced;

b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(v) where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) this dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

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DECLARATION 2: PUBLICATION

1. Chisa, A.L., Mandizvo, T., Odindo, A. and Mafongoya, P., 2025. Effect of Hydropriming on Seedling Growth of Different Bambara Groundnut (Vigna subterranea (L.) Verdc.) Landraces. ***Agronomy***, *15*(6), p.1301.

2. Chisa, A., Odindo, AO.,Mafongoya, PL. and Phophi, MM. 2025. Underutilised legumes for advancing climate-smart agriculture in sub-Saharan Africa**.** ***Legume Science***. **(Under review).**

3. Chisa. A, Mandizvo, T, Odindo, AO, and Mafongoya, PL. 2025. Phenotyping root traits for drought tolerance in Bambara groundnut (Vigna subterranea (L.) Verdc.). ***Frontiers in Plant Science***. **Submitted for review**
4. Chisa. A, Mandizvo, T, Odindo, AO, and Mafongoya, PL. 2025. Structural and physiological seed coat traits across Bambara groundnut (*Vigna subterranea L.)* landraces. ***Heliyon***. **Submitted for review**

ABSTRACT

Agriculture in sub-Saharan Africa (SSA) is increasingly threatened by the impacts of climate change, including prolonged droughts, erratic rainfall, and soil degradation, which undermine food production and nutritional security. While climate-smart agriculture (CSA) offers a framework for enhancing resilience, productivity, and sustainability, much of the attention and research investment has been directed toward major staple crops, which often exhibit limited adaptability to dryland conditions. In contrast, underutilised legumes such as Bambara groundnut (*Vigna subterranea* (L.) Verdc.) present a valuable yet largely untapped opportunity for advancing CSA objectives due to their inherent drought tolerance, adaptability to marginal soils, and rich nutritional profile. Significant knowledge gaps remain regarding key morphological and physiological traits critical for their performance under water-limited environments, hindering their wider adoption, integration into breeding programmes, and inclusion in formal seed systems.

This thesis sought to evaluate the potential of underutilised legumes for climate-smart agriculture by focusing on the characterisation of functional traits in Bambara groundnut that support resilience under water stress. The research comprised three interconnected experimental studies. Firstly, root system architecture was phenotyped across multiple Bambara groundnut landraces grown under contrasting moisture regimes. The experiment revealed significant genotypic variation in traits such as root depth, lateral spread, total root length, and root dry mass. These root traits are key indicators of drought avoidance strategies and are crucial for maintaining water uptake and physiological stability in dryland farming systems. Secondly, seed coat morphology was investigated to understand its role in seed performance. The study demonstrated that differences in seed coat thickness, colour, and permeability significantly influence hydration dynamics, solute leakage, and susceptibility to imbibitional injury, thereby impacting germination speed, uniformity, and seedling vigour. Such findings highlight a critical trade-off between seed protection and rapid emergence, with direct implications for varietal screening and seed quality improvement, particularly in environments characterised by erratic rainfall and variable soil moisture. Thirdly, the effects of hydropriming, a simple, low-cost seed enhancement technique, were assessed to determine its potential in improving germination and early seedling establishment under water stress. The results indicated that specific hydropriming durations, notably 36 hours, improved germination uniformity, reduced mean germination time, and enhanced early growth performance in

selected Bambara groundnut landraces, offering a practical strategy for mitigating establishment challenges in moisture-variable environments.

Collectively, these three experiments demonstrate how root system architecture, seed coat properties, and seed enhancement techniques interact to influence drought adaptation from germination to early growth. Root traits determine the plant’s capacity to capture and use water efficiently, while seed coat characteristics regulate initial hydration and emergence—both foundational for the crop’s establishment. Hydropriming bridges these physiological mechanisms by preconditioning seeds for uniform germination and stronger seedling development. Together, these findings illustrate an integrated resilience strategy within Bambara groundnut that operates across developmental stages, reinforcing its potential as a model legume for climate-smart agriculture. The research contributes to closing critical knowledge gaps regarding the functional traits underpinning drought resilience and provides actionable insights for breeding programmes, seed system improvement, and policies aimed at repositioning underutilised legumes as strategic assets for sustainable food system transformation in SSA.

ACKNOWLEDGEMENTS

The biblical verse that carried me through the final stretch of this PhD journey is from *Psalm 46:5, which says*: *“God is within her, she will not fail.”* Above everything else, I give thanks to God. This PhD study reminded me that, while I may attempt any challenge on my own strength, it is God who will ultimately carry me through the storms, valleys, and into victory. His grace sustained me every step of the way on this long and challenging journey.

To my study supervisors, Prof. Paramu Mafongoya and Prof. Alfred Odindo, thank you so much for walking this academic path with me since my Honours study. Your belief in my potential, your guidance, and your mentorship have shaped not only my research but also the person I have become today. I am forever grateful for your patience, wisdom, and unwavering support

My sincere gratitude also goes to the National Research Foundation (NRF) for the financial support that made this work possible.

To the support staff at the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, your behind-the-scenes efforts made a world of difference. A special thank you especially to Penny Khumalo and Suzanne Kunz for the administrative support, and to Armstrong for always willing to assist with experiments.

To my incredible colleagues: Dr. Takudzwa Mandizvo, Nontuthuko Mdletshe, Barnabas Oluoch, and Nqobile Nkomo. Thank you for your assistance in my research, your encouragement, advice, laughter, and solidarity. Your support meant more than words can say.

To my dear friends: Dr. Marah Chibwana and Dr. Keabetswe Ncube, thank you for creating space for me to be vulnerable. For every moment I needed to vent, cry, pray, or simply be, you were there for me. God knew I needed you both, this journey was manageable because I had you.

To my man, Tatenda Nyika, you had a front-row seat to this entire rollercoaster. Through the highs and the very low lows, you remained my anchor. Thank you for your love, your prayers, your care, and for pushing me when I needed it most. I thank God for you.

Finally, to my family: who are an immeasurable blessing from God. To my mom and dad, Ethel and Ken, to my sister Tapiwa, and to my cousins and aunts, uncles, friends thank you for believing in me. Your love, prayers, and encouragement were my fuel. Knowing I was loved and being rooted for from the home front carried me every step of the way.

DEDICATION

To my dearest parents, Ken and Ethel Chisa:

Twenty-five years ago, you left everything familiar back home in Malawi and came to South Africa in search of a better life for us. It was not always easy, but every sacrifice you made paved the way for me to become the woman that I am today. Your love, strength, and unwavering belief in a brighter future have carried me through this journey.

So, this achievement is not mine alone, it is yours too. What a blessing it is to have you both here to witness this moment.

Zikomo kwambiri. Ambuye apitilize kukudalitsani.

This one is for you.

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CHAPTER 1: GENERAL INTRODUCTION

1.1. Introduction

Prolonged droughts and heat stress, intensified by climate change, stands as one of the most urgent threats to agriculture in the 21st century (Saleem et al., 2024, Vos and Bellù, 2019). This crisis poses urgent and compounding challenges to global food systems, particularly in sub-Saharan Africa (SSA), where smallholder agriculture remains the backbone of rural livelihoods and national economies (Lefe et al., 2024, Adenle and Agboola, 2011). The SSA region is exceptionally vulnerable to climate variability due to its heavy reliance on rainfed agriculture, widespread poverty, and limited adaptive capacity (Kotir, 2011, Nuhu Jinbaani and Wale, 2023). Adaptive capacity refers to the ability of individuals, communities, or systems to adjust, cope, or recover from climate-related shocks and stresses (Siders, 2019, Engle, 2011). In the context of SSA, this capacity is often constrained by inadequate infrastructure, limited access to technologies, weak extension services, poor market integration, and insufficient institutional support all of which reduce farmers' ability to anticipate, prepare for, or respond effectively to climatic risks (Ayanlade et al., 2022, Epule et al., 2023).

According to IPCC (2021), if global mitigation efforts remain inadequate, temperatures could increase by 1.6°C to 6.9°C by the end of the 21st century (Sanderson et al., 2011). These climatic shifts, marked by erratic rainfall, prolonged droughts, and heat stress are already disrupting crop production and threatening food and nutritional security across the continent. At the same time, SSA continues to face issues of food insecurity and undernutrition, exacerbated by climate-induced yield losses and a reliance on a narrow range of staple crops (Harper et al., 2022, Christian and Dake, 2022, Nel and Steyn, 2022). These interlinked crises underscore the urgent need for transformative agricultural strategies that enhance resilience to climate change, ensure sustainable food production, and reduce environmental impact (Santos et al., 2023, Gondwe et al., 2023).

An agricultural strategy that has gained global interest to address the crisis of climate change is climate-smart agriculture (CSA) (FAO, 2010, FAO, 2019). It has emerged as a guiding framework that integrates three interrelated objectives: (i) increasing agricultural productivity, (ii) enhancing resilience to climate stress, and (iii) reducing greenhouse gas (GHG) emissions (FAO, 2010). CSA also contributes to several Sustainable Development Goals (SDGs), notably SDG 2 (Zero Hunger), SDG 13 (Climate Action), and SDG 3 (Good Health and Well-being)

(FAO, 2019). Yet, the practical implementation of CSA remains limited, hindered by fragmented institutional support (Sanogo et al., 2023), weak seed and market systems (Louwaars et al., 2013), and low uptake of innovations beyond pilot phases (Dossou-Yovo et al., 2024).

CSA offers a promising framework, its implementation remains skewed toward major staple crops such as maize (*Zea mays*), rice (*Oryza sativa*), and soybean (*Glycine max*), which are increasingly vulnerable to rising temperatures, erratic rainfall, and declining soil fertility (Poole et al., 2022, Kızıldeniz et al., 2023). These climate-sensitive crops dominate food systems in sub-Saharan Africa (SSA), yet they are poorly suited to the region's dryland ecologies and offer limited nutritional diversity.

In contrast, Bambara groundnut (*Vigna subterranea (L.) Verdc.),* a drought-resilient, nutrient-rich legume indigenous to Africa, presents a compelling alternative. As an underutilised crop with inherent adaptability to marginal environments and low external input needs, bambara groundnut (BGN) has received growing scientific attention. While other legumes such as tepary bean and pigeon pea also show promise, this study focuses exclusively on BGN due to its strong alignment with CSA objectives and its potential to address multiple challenges facing smallholder farmers in SSA.

From a scientific perspective, the performance of BGN within climate-smart agriculture remains underexplored particularly seed traits that influence germination, storability, and early establishment (Mayes et al., 2019, Olanrewaju et al., 2022). While BGN is valued for its drought resilience and nutritional benefits, limited research has investigated how specific seed coat characteristics, such as colour, thickness, and permeability influence its viability and vigour. Mandizvo and Odindo (2019) found that darker, thicker seed coats offered greater resistance to imbibitional damage, while lighter-coloured seeds exhibited higher viability but lower vigour. However, most studies in this area have been narrow in scope, often limited to a few genotypes, and lack a comparative or mechanistic understanding of how these seed coat traits function under varying environmental conditions. Further, there is little clarity on how these traits interact with external stressors like drought or contribute to field emergence and seedling robustness in low-input systems. These structural traits affect water uptake, membrane stability, and overall seed performance (Gerrano et al., 2021), yet their physiological basis and practical implications for breeding or seed quality improvement remain poorly defined. A better understanding of such traits is essential for enhancing crop establishment, particularly in resource-constrained farming systems.

Beyond seed traits, below-ground characteristics also play a crucial role in crop resilience under stress conditions. In this regard, root system architecture (RSA) plays a central role in determining plant adaptability to water-limited environments (Xie et al., 2016). Root traits influence water and nutrient uptake, anchorage, and interactions with soil microbes, yet are frequently neglected in breeding and agronomic trials (Poorter et al., 2012, Mateva et al., 2020). Studying RSA in underutilised legumes can offer insights into the mechanisms of drought avoidance and tolerance.

Another area with potential is seed priming, especially hydropriming which is a method of soaking of seeds in water before sowing (Berchie et al., 2010). This is a simple, low-cost physiological enhancement technique that pre-activates seed metabolism and improves emergence, vigour, and stress tolerance (Sajjan et al., 2017, Kumeera et al., 2018). Its application to BGN and other underutilised legumes have proven to be beneficial. Chisa et al. (2025) reported that hydropriming, particularly for 36 hours, showed promise in promoting early growth in BGN. However, despite evidence of its benefits, limited studies have examined how hydropriming influences the physiological responses of different Bambara groundnut genotypes, especially under varying water regimes. This gap is critical, as genotype-specific responses may determine the effectiveness of priming under field conditions.

This thesis investigates the performance of BGN under water stress, focusing on traits that support climate-smart agriculture principles. While the literature review considers other underutilised legumes, such as tepary bean (*Phaseolus acutifolius)* and pigeon pea (*Cajanus cajan*), due to their relevance in dryland farming systems, the empirical work of this study narrows its focus exclusively to BGN. This crop was selected because of its well-documented drought tolerance, nutritional potential, and adaptability to marginal environments in sub-Saharan Africa (Nwadi et al., 2020, Tan et al., 2020, Rahmah et al., 2020). However, despite these advantages, BGN remains significantly under-researched particularly in terms of its early-stage traits such as root architecture, seed coat morphology, and response to seed priming. These gaps limit its inclusion in formal seed systems, breeding programmes, and climate-resilient agricultural strategies. Accordingly, this thesis comprises three interlinked studies centred on BGN: the first characterises root traits under water stress; the second investigates seed coat features related to germination and vigour; and the third evaluates the effects of hydropriming on seedling establishment and drought resilience.

By consolidating evidence from these complementary dimensions, this research supports a broader agenda of repositioning underutilised legumes as climate-smart crops that can improve resilience, food security, and sustainability in SSA's dryland farming systems. This research also contributes to knowledge of underutilised climate smart legumes that can build a stronger case for their mainstreaming in national and regional agricultural strategies. With the potential to bridge the gap between scientific knowledge, farmer practice, and policy transformation.

1.2. Problem statement

Although BGN is widely recognised for its resilience to drought and its suitability for low-input systems, fundamental knowledge gaps limit its improvement and broader adoption. In particular, the physiological and morphological traits that influence early-stage performance under water stress remain poorly understood. Three areas are especially under-researched: root system architecture, which governs water uptake and drought avoidance; seed coat morphology, which affects water absorption and germination; and the potential of seed priming to enhance seedling establishment.

Empirical data on these traits are limited, partly due to methodological challenges, such as the difficulty of observing root systems and the genetic variability of BGN landraces. Without this foundational knowledge, it is difficult to develop breeding, agronomic, or seed enhancement strategies tailored to the crop's unique attributes. This study addresses these gaps by systematically investigating root traits, seed coat characteristics, and priming responses in BGN, with the aim of informing climate-resilient crop improvement efforts.

1.3. Justification

Sub-Saharan Africa faces escalating food and nutrition insecurity, with over 281 million people undernourished and smallholder farmers, who produce up to 70% of the region's food, particularly vulnerable to climate shocks, soil degradation, and erratic rainfall (FAO, 2023, Sithole and Olorunfemi, 2024). BGN, an underutilised legume with proven drought tolerance, high nutritional content, and low input requirements, is well-suited to these conditions and aligns strongly with climate-smart agriculture objectives (Cheng et al., 2017, Nadeem et al., 2019). Despite its potential, it continues to receive limited attention in structured crop improvement programmes, resulting in a lack of targeted research, breeding efforts, and formal support mechanisms to enhance its adoption (Ferreira et al., 2021, Odeku et al., 2024).

A key limitation is the absence of empirical data on the physiological and morphological traits that underpin BGN's performance under water stress, particularly during early growth stages. RSA, central to water acquisition and drought avoidance, remains underexplored due to the methodological complexity of root phenotyping (Lynch et al., 2021, Faverjon et al., 2019, Mateva et al., 2020). In parallel, seed coat traits such as thickness, colour, and permeability which influence water absorption, dormancy, and seedling vigour have received minimal research attention, despite their established relevance for germination and storage (Mandizvo and Odindo, 2019, Jarrar et al., 2023).

Furthermore, seed enhancement techniques like hydropriming, which have demonstrated efficacy in improving germination and early growth in other crops, remain insufficiently studied in BGN, especially across its genetically diverse landraces (Sajjan et al., 2017, Marthandan et al., 2020). This gap is particularly problematic in SSA's dryland systems, where poor crop establishment under water-limited conditions is a persistent constraint to productivity.

This study responds directly to these gaps by investigating three interrelated early-stage traits in BGN: (1) root architecture under water stress, (2) seed coat morphological characteristics, and (3) the effects of hydropriming on germination and early establishment. These traits are foundational to improving drought resilience, stand establishment, and yield reliability in low-input smallholder systems. By generating empirical data on these overlooked functional traits, the research contributes to repositioning BGN as a strategic crop for climate-resilient, nutrition-sensitive agriculture in SSA, while supporting the broader objectives of Sustainable Development Goals 2 (Zero Hunger) and 13 (Climate Action).

1.4. Aim

To assess the potential of underutilised legumes for climate-smart agriculture by examining and characterising traits that support resilience under water stress.

1.4.1 Research questions

I. How do variations in root architectural traits among Bambara groundnut genotypes influence drought tolerance and overall climate resilience?
II. How do differences in seed coat characteristics affect germination performance and seedling vigour under variable moisture conditions?
III. To what extent can hydropriming enhance early establishment and improve stress resilience in Bambara groundnut?

1.4.2 Specific objectives

The following are the specific research objectives for the study:

I. To characterise the root architecture of Bambara groundnut genotypes and determine its relationship with drought tolerance and climate resilience.
II. To assess the influence of seed coat traits on germination and seedling vigour under contrasting water regimes.
III. To evaluate the effectiveness of hydropriming in enhancing early establishment and improving stress resilience across Bambara groundnut genotypes

Study Limitations

This study was limited by its experimental scope and controlled environment. All trials were conducted under greenhouse conditions, which, while enabling precise control of treatments, may not fully capture the variability of field environments. The study also focused on a small set of Bambara groundnut landraces and on early growth stages(germination, emergence, and seedling development) rather than full-season performance. Consequently, field-based studies involving more diverse genotypes and multi-season trials are required to validate these findings and determine their broader agronomic relevance under varying environmental and management conditions.

1.5. Thesis structure

Chapter 1: Introduction

This chapter provides an overview climate change's background and impact on agriculture, establishing the need for sustainable practices. It presents the problem statement, focusing on the unsustainable nature of current agricultural practices and the limited climate resilience of commonly consumed legumes. The chapter outlines the research questions and objectives, emphasizing the exploration of alternative climate-smart legumes. The significance of the study is discussed, along with its scope and limitations, setting the stage for the subsequent chapters.

Chapter 2: Literature review

This chapter reviews existing literature on climate-smart agriculture and its relevance to the study. It explores the adaptability, nutritional value, and climate resilience of the tepary bean, Bambara groundnut, and pigeon pea. This chapter also examines root architectural traits and their importance in drought tolerance, the effects of drought stress on yield and nutritional quality, and the potential of priming effects to enhance plant stress tolerance. The literature review provides a theoretical foundation for the experimental studies presented in the following chapters.

Chapter 3: Root phenotyping study

This chapter focuses on root phenotyping as a key factor in understanding plant resilience to climate change. It introduces the concept of root phenotyping and its relevance to climate resilience. The results section presents findings on root architectural traits and their relationship with drought tolerance. The discussion explores how these root traits can enhance climate resilience, forming the basis for the drought stress study in the next chapter.

Chapter 4: Seed Coat Trait Study in Bambara Groundnut

This chapter investigates the physical and physiological characteristics of seed coats across selected BGN landraces. It focuses on key traits such as seed coat colour, thickness, permeability, and structural integrity, which influence hydration patterns, solute leakage, and susceptibility to imbibitional damage. The study assesses how these traits affect germination rate, seedling vigour, and early establishment under controlled conditions. The findings contribute to understanding intra-species variability in seed quality and provide insights into how seed coat morphology may be harnessed to improve crop performance in resource-limited and drought-prone environments.

Chapter 5: Priming effects on Bambara groundnut

This chapter explores the potential of priming to enhance drought tolerance. It introduces hydropriming and its role in improving stress tolerance. The results reveal that priming can be a viable approach for uniform crop establishment. The discussion demonstrates how priming can effectively improve the resilience of climate-smart legumes.

Chapter 6: Conclusions

This final chapter synthesizes the key findings from the root phenotyping, seed coat, and priming studies, illustrating how each aspect contributes to developing climate-smart agriculture practices. It highlights the overall implications for enhancing food security in SSA through underutilized legumes. Recommendations for future research are provided, along with a discussion of the contributions to knowledge and practice, drawing connections to the broader context of sustainable agriculture and climate resilience.

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CHAPTER 2: UNDERUTLISED LEGUMES FOR ADVANCING CLIMATE-SMART AGRICULTURE IN SUB-SAHARAN AFRICA

Abstract

Sub-Saharan Africa faces intersecting challenges of food insecurity, malnutrition, and climate variability, exacerbated by the predominance of rainfed agriculture and limited input use. Climate-smart agriculture (CSA) offers a framework to address these issues through increased productivity, enhanced resilience, and reduced environmental impact. Underutilised legumes such as Bambara groundnut (*Vigna subterranea*), tepary bean (*Phaseolus acutifolius*), and pigeon pea (*Cajanus cajan*) present untapped opportunities for advancing CSA objectives. This review synthesises current knowledge on their physiological and agronomic traits such as: drought tolerance, nitrogen fixation, short growth cycles, and seed priming responses that support climate adaptation in dryland systems. Despite their potential, these legumes remain marginal in formal seed systems, research investment, and public policy. Key gaps include limited field-based evaluations, underdeveloped seed and market systems, and weak institutional support. The review suggests for a whole-of-system approach linking research, extension, and policy to scale these crops as strategic assets for resilient, inclusive, and nutrition-sensitive food systems in sub-Saharan Africa.

Keywords: climate change, Bambara groundnut, pigeon pea, tepary bean, drought resilience, seed priming, sustainable food systems

2.1. Introduction

The escalating climate crisis poses urgent challenges to global food systems, with sub-Saharan Africa (SSA) being particularly vulnerable due to its reliance on rainfed agriculture and the prevalence of resource-constrained smallholder farming (Lefe et al., 2024). The Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report (IPCC, 2021) projected that, in the absence of emission-reduction strategies (IPCC, 2023), global temperatures could rise by 1.6°C to 6.9°C by the end of the twenty-first century (Sanderson et al., 2011) . In SSA, increasing climate variability, which is marked by more frequent droughts and erratic rainfall, has already begun to disrupt agricultural productivity and rural livelihoods (Kotir, 2011).

At the same time, the region continues to grapple with the dual challenges of persistent food insecurity and malnutrition (Harper et al., 2022, Christian and Dake, 2022, Nel and Steyn, 2022, Santos et al., 2023, Gondwe et al., 2023). These converging threats underscore the need for adaptive agricultural strategies that simultaneously enhance resilience, improve food and nutrition security, and minimise environmental impacts. In this context, climate-smart agriculture (CSA) has emerged as a guiding framework, with three key objectives, (i) increase productivity, (ii) build resilience to climate stress, and (iii) reduce greenhouse gas emissions (FAO, 2010).

CSA is closely aligned with several of the United Nations Sustainable Development Goals (SDGs) (FAO, 2019), particularly SDG 2 (Zero Hunger), SDG 13 (Climate Action), SDG 12 (Responsible Consumption and Production), and SDG 3 (Good Health and Well-being). With less than a decade remaining until the 2030 deadline, implementing locally relevant, nutrition-sensitive, and environmentally sound interventions is imperative. However, while many CSA-aligned innovations exist on paper or in trial settings (Long et al., 2016, Dossou-Yovo et al., 2024, Makate, 2019), their practical uptake often falls short, due in part to institutional silos (Louwaars et al., 2013), weak value chains (Louwaars and De Boef, 2012), limited market demand (Dossou-Yovo et al., 2024), and fragmented policy support (Sanogo et al., 2023).

Underutilised legumes such as Bambara groundnut (*Vigna subterranean* (L.) (Verdc.), tepary bean (*Phaseolus acutifolius* A. Gray), and pigeon pea (*Cajanus cajan* (L.) offer significant but underexplored potential for advancing CSA objectives in dryland SSA (Mijena et al., 2024, Rani et al., 2023). These crops adapt well to harsh environments, require minimal external inputs, and provide important nutritional benefits. Their ability to fix atmospheric nitrogen, tolerate drought, and contribute to diversified diets aligns closely with the core principles of CSA. Yet, despite growing scientific interest, they remain neglected in formal seed systems, largely absent from commercial markets, and rarely prioritised in policy or private sector investment (Rani et al., 2023). Their promotion has been heavily skewed toward smallholder and subsistence contexts, which, while important, limits their visibility and potential as mainstream crops that can benefit the wider food system (Conti et al., 2019).

Although the primary research focus of this thesis is on Bambara groundnut, this literature review deliberately adopts a broader lens by including tepary bean and pigeon pea. This comparative perspective is intended to situate Bambara groundnut within the wider context of underutilised legumes, highlighting shared challenges and contrasting traits that inform breeding targets and agronomic strategies. Insights from these related species help identify unique constraints and opportunities specific to Bambara groundnut, thereby sharpening the research focus and rationale of this thesis.

This review investigates how these three legumes can contribute to the advancement of CSA in dryland systems. It synthesises current knowledge on their physiological and agronomic traits related to climate resilience, including root system architecture, water-use efficiency, and osmotic adjustment. In addition, the review evaluates the use of seed priming, particularly for Bambara groundnut, as a low-cost technique to improve crop establishment and performance under drought-prone conditions.

Although these legumes strongly align with CSA principles, research on their practical integration into climate-resilient farming systems remains limited. For crops like Bambara groundnut, early growth challenges such as poor emergence and slow establishment persist, yet seed priming as a low-cost intervention remains underexplored, especially under field conditions across SSA. In contrast, tepary bean and pigeon pea show inherent vigour during establishment but have received relatively less attention in physiological trait analysis despite their proven drought tolerance.

By consolidating existing evidence and identifying areas for future research, such as seed enhancement techniques for Bambara groundnut, or the need for multi-trait evaluations under real-world conditions, the review contributes a targeted framework for repositioning underutilised legumes as viable, underused assets in advancing CSA objectives. It also supports broader progress toward the SDGs, while acknowledging the urgent need to connect smallholder realities with national and regional food system strategies.

2.2. Climate-Smart Agriculture

CSA has emerged as a leading framework for addressing the interconnected challenges of food insecurity, climate change, and environmental degradation in agriculture. Its threefold objective is to increase agricultural productivity sustainably, enhance resilience to climate-related shocks, and reduce greenhouse gas emissions, which renders it particularly relevant to dryland farming systems in sub-Saharan Africa (FAO, 2010).

The FAO (2019) report underscores CSA as a holistic and integrative approach that directly aligns with the 2030 Agenda for Sustainable Development, notably SDGs 2, 3, 12, and 13. It affirms CSA's three core pillars: (i) productivity enhancement, (ii) climate resilience, and (iii) mitigation of greenhouse gas emissions, as critical levers for transforming food systems in dryland regions. CSA is especially important in developing contexts such as SSA, where agriculture remains central to GDP and livelihoods, yet is highly vulnerable to climate variability (Abegunde et al., 2019). For SSA, where the effects of climate change are already compounding structural food system challenges, CSA offers a pathway to align climate adaptation with nutrition-sensitive and locally grounded interventions (Talucder et al., 2024).

CSA encompasses adaptive agricultural practices that promote sustainable productivity gains while trying to optimise benefits and reduce trade-offs across its core objectives (Lipper et al., 2014). When adopted holistically within farming systems, CSA practices provide multiple benefits for smallholder farmers, including enhanced resilience, livelihoods, and incomes (Totin et al., 2018). Fundamentally, CSA is designed to support farmers in adapting to climate change while mitigating its potential negative impacts on agricultural production and rural livelihoods (FAO, 2013).

Farmers in SSA have adopted various strategies to enhance productivity and adapt to changing climatic conditions, many of which align with CSA principles (Serdeczny et al., 2017). In regions with limited rainfall, for example, farmers are increasingly replacing water-intensive crops with more drought-tolerant alternatives (Ngwira et al., 2012). In flood-prone areas, there has been a shift towards short-cycle crops, while other adaptation strategies include crop diversification, altered planting dates, and mixed cropping systems (Ngwira et al., 2013). These practices are evidence of the multidimensional goals of CSA by enhancing both productivity and resilience under climatic stress.

There is growing recognition that underutilised crops, particularly those resilient to drought, low-input conditions and soil degradation, can significantly contribute to achieving CSA outcomes (Rani et al., 2023) . Though often overlooked in formal agricultural systems, their biological traits and nutritional value offer promising solutions to address climatic and food system vulnerabilities (Conti et al., 2019).

Legumes have garnered attention due to their capacity to fix atmospheric nitrogen, improve soil health, diversify diets, and serve as important protein sources. These traits align with CSA's productivity, resilience, and mitigation pillars (Mijena et al., 2024).

The following section explores the case for focusing on underutilised legumes in CSA. This review highlights three key examples: Bambara groundnut, tepary bean and pigeon pea, and explains their potential as climate-smart crops for dryland regions.

2.3. The Potential of Underutilised Legumes in CSA

Underutilised legumes include a wide range of species that have historically received limited attention in research, breeding, and agricultural development strategies, despite their adaptation to marginal environments and contribution to food and nutritional security (Ayilara et al., 2022, Bhat and Karim, 2009, Cheng et al., 2019). Examples of these legume species include African yam bean (*Sphenostylis stenocarpa Hochst. ex A. Rich.),* Kersting's groundnut (*Macrotyloma geocarpum (Harms) Maréchal & Baudet*), marama bean (*Tylosema esculentum (Burchell) A. Schreiber*), cowpea (*Vigna unguiculata (L.) Walp*), jack bean (*Canavalia ensiformis (L.) DC*), and lima bean (*Phaseolus lunatus L.)*(Ayenan and Ezin, 2016, Bhat and Karim, 2009, Padulosi et al., 2013). Each legume has unique climate-resilient traits and nutritional profiles that can contribute to more diversified, sustainable food systems in SSA.

This review focuses on Bambara groundnut, tepary bean, and pigeon pea for three key reasons. First, each crop has a growing, though still limited, body of scientific literature examining traits relevant to CSA, such as drought tolerance, nitrogen fixation, and seed nutrient composition. Second, they represent varied agroecological origins (Figure 2.0.1) originating respectively from Africa, North America, and South Asia. These legumes exemplify parallel evolution in their adaptation to arid and semi-arid environments (Moghaddam et al., 2021). Despite their distinct phylogenetic lineages and geographic origins, they have independently developed similar adaptive traits such as deep rooting systems, efficient water use, and robust nitrogen-fixing capabilities, these traits enable them to thrive under drought and heat stress conditions (Upadhyaya et al., 2012, Marthandan et al., 2020). This convergence offers valuable insights into varied adaptation pathways and the potential for cross-regional strategies in legume improvement. Third, all three crops show promise for integration into dryland smallholder systems, yet remain underrepresented in commercial seed systems, extension programs, and national agricultural research agendas.

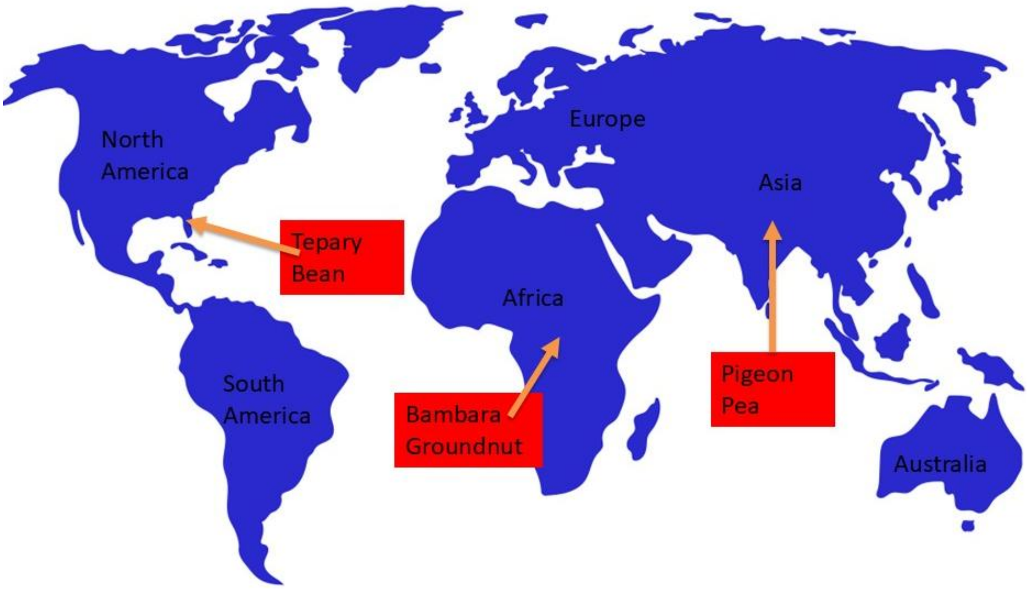

Figure 2.0.1: Agroecological origins of the focal legumes (map sourced from freepix copyright free)

2.3.1 Bambara Groundnut

Bambara groundnut is an indigenous African legume well adapted to dryland farming systems. It has the ability to thrive in nutrient-poor soils, under low-input conditions and its noted for its high drought tolerance (Mayes et al., 2019). In terms of overall seed composition, Bambara groundnut seeds typically contain approximately 60–65% carbohydrates (mainly starch), 18–24% protein, and around 6–7% fat, placing it nutritionally in the mid-range of grain legumes but significantly higher in protein and micronutrients than cereals (Hlanga et al., 2021, Tan et al., 2020). The seeds are the primary edible part and can be consumed fresh or dried, offering dietary versatility particularly suitable for subsistence farmers in arid and semi-arid regions (Tan et al., 2020).

Agronomically, Bambara groundnut exhibits several traits that align with CSA objectives. Its root system is both deep and extensive, and dependent on the agronomic region where its grown. Mateva et al. (2020) reports that landraces from drier regions such as sub-Saharan Africa generally have longer taproots and greater root length distribution in deeper (60 to 90 cm) soil depths. In contrast, landraces from wetter regions like Southeast Asia and West Africa exhibited relatively shallow and highly branched root growth closer to the soil surface. The crop has a relatively dense, closed canopy under optimal spacing, which helps reduce soil evaporation and contributes to improved water-use efficiency and weed suppression (Olanrewaju et al., 2022). Despite these favorable traits, the crop is still largely cultivated as genetically diverse landraces, with limited availability of improved or commercial varieties, which constrains breeding efforts and yield consistency (Aliyu et al., 2014). A notable agronomic constraint is its hard seed coat, which delays germination and reduces emergence rates, a barrier particularly problematic under erratic rainfall and shortened planting windows (Mandizvo and Odindo, 2019).

Bambara groundnut is a fast-growing crop that requires warm temperatures and cannot tolerate frost during the growing season. Depending on the variety, it typically matures within 110 to 150 days (Gerrano et al., 2021). These characteristics make it an ideal candidate for seed priming interventions, which can improve early emergence and seedling vigour, and further enhance its suitability for integration into low-input, climate-resilient agricultural systems.

2.3.2 Tepary Bean

Tepary bean, native to the arid regions of the south-western United States and north-western Mexico, is increasingly recognised as a climate-resilient legume (Porch et al., 2017). It is predominantly cultivated in arid and semi-arid environments due to its tolerance to heat and drought (Rao et al., 2013). The crop is also resistant to many pests and diseases and is widely used in common bean (*Phaseolus vulgaris*) improvement programmes as a source of genetic variation for abiotic stress tolerance.

In sub-Saharan Africa, tepary bean are cultivated mainly by smallholder farmers under poor soils and low-input conditions (Jiri and Mafongoya, 2016). Research has highlighted several advantageous agronomic traits of the species that make it suitable for dryland farming systems. For example, it has a short growth cycle, with emergence occurring within 5–10 days and maturity typically reached within 60 to 120 days (Jiri and Mafongoya, 2016, Ghadimian et al., 2021). Tepary beans also develop a deeper taproot compared to common bean; while the latter reaches depths of 0.5 to 1 meter, tepary bean roots can extend up to twice as deep, enhancing its ability to access subsoil moisture (Burridge et al., 2020). In addition, it demonstrates high water-use efficiency, a critical trait under conditions of moisture stress (Mhlaba et al., 2018). Although these attributes confer inherent resilience, productivity remains limited where unimproved or recycled seed is used. The development and adoption of improved varieties could significantly enhance performance and yield consistency under such marginal conditions.

Tepary bean fixes atmospheric nitrogen through symbiosis with *Rhizobium* sp. strain R3254, contributing up to 260 kg N ha^{-1} after inoculation and improving soil fertility (Ullah, 2010). Nutritionally, it is rich in protein, with content ranging from 23% to 25%, comparable to other grain legumes (Mwale et al., 2020). The dry grains are consumed in stews, soups, or with maize, while the leaves, though tougher, are also edible (Albala, 2011).

Despite its potential, tepary bean remains underutilised in formal agricultural systems. Its resilience, soil-enriching capacity, and nutritional value align well with the pillars of climate-smart agriculture, warranting greater attention in research, breeding, and policy to support sustainable farming in resource-limited settings**.**

2.3.3 Pigeon Pea

Pigeon pea is a drought-resilient legume originally domesticated in Asia but now widely cultivated in tropical and subtropical regions, particularly across sub-Saharan Africa (Saxena, 2008). It thrives in marginal environments characterized by low soil fertility and erratic rainfall, making it well suited for smallholder farming systems (Chisa et al., 2021). One of its notable traits is a deep root system, reaching depths of 1 to 2 meters, which allows the plant to access subsoil moisture during dry periods (Fernandes et al., 2023). Pigeon pea is also commonly intercropped with cereals such as maize and sorghum, improving land-use efficiency and contributing to system resilience through complementary nutrient and water use (Fernandes et al., 2023).

Pigeon pea contributes significantly to soil health, functioning as a biological soil ameliorant. It enhances soil nitrogen levels through biological nitrogen fixation and leaf litter, contributing between 40 and 60 kg N ha^{-1} to the soil annually (Ansari and Mahmood, 2017, Kizito, 2018). The crop performs well on degraded soils and can stabilize yields under moderate drought conditions (Bakala et al., 2024). A key feature of pigeon pea is its wide range of maturity durations, which vary by cultivar. Early-maturing varieties reach maturity in approximately 90–145 days, while medium and long-duration types can take up to 250–300 days (Saxena, 2008, Singh et al., 2018). Long-duration cultivars, although beneficial in extended growing seasons, are vulnerable to winter frost damage, particularly when grown in areas with late-season cold spells. In contrast, short-duration, high-yielding cultivars, many developed by ICRISAT are better suited to multiple cropping systems under both rainfed and irrigated conditions. These genotypes are less sensitive to photoperiod, can escape end-of-season drought, and offer flexibility in cropping calendars by allowing farmers to grow a second crop such as wheat, barley, mustard, or chickpea after harvest (Singh et al., 2018).

Nutritionally, pigeon pea is a valuable legume, particularly for regions where diets are predominantly cereal-based and prone to protein-energy malnutrition. The dry seeds contain approximately 20–22% protein, offering a vital plant-based protein source for low-income households (Adjei-Nsiah, 2012). In addition to protein, pigeon pea is rich in dietary fibre (about 15 g per 100 g), which supports digestive health and glycaemic regulation (Haji et al., 2024). The seeds also provide essential micronutrients, including iron (5.2 mg/100 g), magnesium (183 mg/100 g), phosphorus (367 mg/100 g), and potassium (1,392 mg/100 g), all of which play important roles in oxygen transport, neuromuscular function, and bone mineralisation (Kunyanga et al., 2013, Haji et al., 2024).

The seeds are commonly consumed boiled, split as dhal, or incorporated into traditional dishes such as stews and porridges. Additionally, in some regions, the young pods and leaves are eaten as vegetables, contributing to dietary diversity and increased micronutrient intake (Fernandes et al., 2023; Chisa et al., 2021).

Although ICRISAT has progressed in breeding for stress tolerance and disease resistance (Varshney et al., 2010), most farmers still rely on unimproved landraces with suboptimal traits (Hluyako et al., 2017). Greater investment in breeding, farmer outreach, and value chain development is essential to unlock pigeon pea's full potential as a climate-smart crop in sub-Saharan Africa.

Together, these three legumes illustrate the diverse pathways through which underutilised crops can support the CSA agenda (Table 2.0.1). The following section will examine the physiological and agronomic traits that underpin their performance under stress and highlight their alignment with the CSA pillars of productivity, resilience, and mitigation.

Table 2.0.1 Summary of the comparative traits of selected legumes

Trait/Function	Bambara Groundnut	Tepary Bean	Pigeon Pea
Native origin	Africa	Americas	Africa/Asia
Drought tolerance	High	Very High	Moderate–High
Root architecture	Deep, extensive	Deep	Deep
Nitrogen fixation	Yes	Yes	Yes
Nutritional value	High protein, balanced amino acids	High protein, micronutrients	High protein, fibre
Growth cycle	Medium (90–150 days)	Short (60–90 days)	Medium-long (90–300 days)
Adaptability to poor soils	High	Moderate–High	High
Canopy cover / soil moisture use	Closed canopy, reduces evaporation	Moderate canopy	Moderate canopy
Seed priming response	Good	N/A	Limited
Use in intercropping	Limited	Limited	Common with cereals

2.4. Key Traits Supporting Climate-Smart Functions

Underutilized legumes exhibit key physiological and agronomic traits such as deep root systems, osmotic adjustment, stomatal regulation, nitrogen fixation, short growth cycles, and seed priming response that make them highly suitable for dryland farming in sub-Saharan Africa. These traits are particularly aligned with the goals of climate-smart agriculture (CSA) (Figure. 2.0.2), which aims to increase productivity, enhance resilience to climate variability, and reduce environmental impact. In contexts of erratic rainfall, poor soils, and limited inputs, these traits are not just advantageous but essential for crop survival, rapid establishment, and consistent yields under stress.

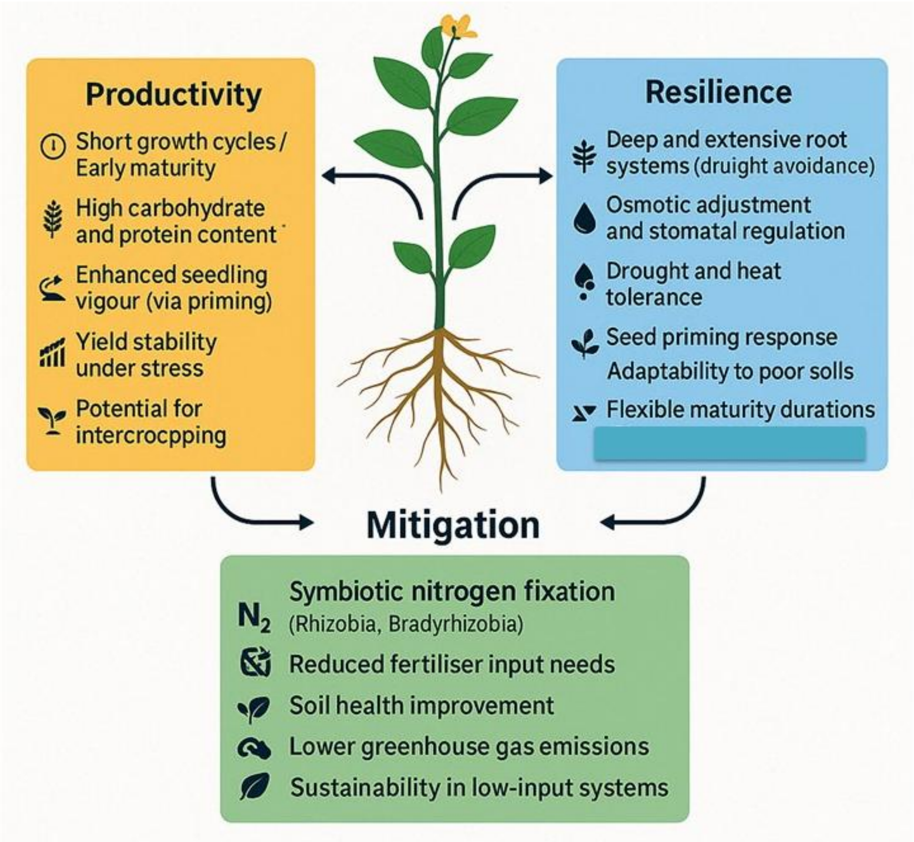

Figure 2.0.2: Functional traits of underutilized legumes aligned to climate smart objectives (adapted from (Ayilara et al., 2022))

This section explores how these traits contribute to one or more CSA pillars, offering insight into their functional value and practical relevance. It also identifies key knowledge gaps, particularly in comparative field research and varietal performance, that must be addressed to maximise the full potential of underutilised legumes in sustainable agriculture.

2. 4.1 Deep Root Systems

Deep and extensive root systems are among the most critical drought-resilience traits observed in underutilised legumes such as Bambara groundnut, tepary bean, and pigeon pea. These systems allow the crops to access water from deeper soil horizons, enhancing physiological stability and yield maintenance under moisture stress (Poorter et al., 2012). For instance, Bambara groundnut landraces from drier regions of sub-Saharan Africa have demonstrated root penetration depths ranging from 60 to 90 cm, with higher root length density in deeper soil layers compared to landraces from wetter regions, which tend to have shallower, more branched roots (Mateva et al., 2020). Similarly, tepary bean taproots have been reported to extend up to 2 metres, twice as deep as those of common bean, enabling superior access to subsoil moisture and improving drought escape (Burridge et al., 2020).

Pigeon pea also develops a deep taproot system, reaching 1–2 metres, which allows it to maintain transpiration and growth during prolonged dry spells (Fernandes et al., 2023) . This rooting strategy, when combined with its ability to persist in degraded soils, positions pigeon pea as a viable legume for agroecologies experiencing erratic rainfall patterns.

These root traits such as rooting depth, root length density, and vertical distribution directly influence water-use efficiency (WUE) and drought adaptation, particularly in dryland farming systems where rainfall is both unpredictable and poorly distributed across the growing season (Faverjon et al., 2019, Abdelhamid, 2010). For example, the deep rooting architecture of tepary bean contributes to its high WUE under limited irrigation and minimal soil fertility (Mhlaba et al., 2018).

Despite their evident ecological value, the root systems of many underutilised legumes remain understudied, especially under field conditions in sub-Saharan Africa. Challenges such as limited access to high-throughput root phenotyping platforms and variability in root development across environments constrain breeding efforts for drought-adaptive ideotypes (Abdelhamid, 2010). Investing in root phenotyping research including the use of tools like rhizotrons, minirhizotrons, and image-based platforms, would enable a better understanding of genotypic differences and their interaction with agroecological zones. Moreover, insights into root system architecture could inform agronomic decisions, such as plant spacing, soil amendment strategies, and intercropping arrangements, to optimise moisture capture and improve system-level resilience (Mayes et al., 2019, Mateva et al., 2020).

By advancing root trait characterisation in these legumes, researchers and policymakers can better align breeding priorities and management practices with the productivity, resilience, and mitigation pillars of climate-smart agriculture.

2. 4.2 Osmotic Adjustment and Stomatal Regulation

In addition to structural adaptations, underutilised legumes such as Bambara groundnut, tepary bean, and pigeon pea exhibit a range of physiological mechanisms that enhance their resilience under drought and heat stress (Rao et al., 2013). Among these, osmotic adjustment and stomatal regulation play central roles in maintaining plant function when water is limited.

Osmotic adjustment involves the active accumulation of solutes such as proline, sugars, and inorganic ions, within plant cells to maintain cell turgor pressure (Zivcak et al., 2016). This process enables continued cell expansion and delays wilting under low water availability

(Tabassum et al., 2018). Stomatal regulation, on the other hand, governs gas exchange and water loss by adjusting the opening and closing of stomata in response to environmental signals (Kaiser and Paoletti, 2014). Rapid stomatal closure during water stress reduces transpirational water loss while helping to protect internal leaf structures (Marthandan et al., 2020).

While these mechanisms are well documented in cereals and major legumes like wheat, maize, and soybean, they remain less frequently studied in underutilised species. However, emerging research suggests that these processes may confer unique and significant adaptive advantages in crops like Bambara groundnut, tepary bean, and pigeon pea, particularly under the resource-constrained and variable conditions typical of smallholder systems in sub-Saharan Africa.

For example, in Bambara groundnut, certain genotypes have demonstrated enhanced proline accumulation and more efficient stomatal closure under terminal drought stress (Kundy, 2019). These traits enable the crop to sustain photosynthetic activity at lower relative water content, delaying physiological shutdown and allowing continued growth and grain filling during dry periods (Muhammad et al., 2016). In practical terms, this means certain Bambara groundnut can maintain productivity even under severe late-season drought, making it a reliable option for regions with erratic rainfall.

Tepary bean exhibits a conservative water-use strategy, characterised by lower stomatal conductance and high intrinsic water-use efficiency (Mhlaba et al., 2018, Porch et al., 2017). This means the plant loses less water through transpiration while maintaining adequate carbon fixation, allowing it to survive prolonged droughts without significant yield penalties. Such traits are especially valuable in arid regions where water is scarce and irrigation infrastructure is lacking.

In pigeon pea, stomatal sensitivity enables the plant to respond quickly to atmospheric dryness (Lobato et al., 2021). By closing its stomata during, pigeon pea minimises transpirational loss while still supporting canopy cooling and reproductive development, even under high temperatures (Bakala et al., 2024). This mechanism protects critical growth stages like flowering and pod setting from heat stress, which can otherwise lead to flower abortion and yield loss in more sensitive crops.

Beyond stomatal responses, these legumes also activate a range of hormonal and morphological adjustments under stress, such as reducing leaf surface area, increasing root-to-shoot ratios, and modulating levels of abscisic acid (ABA) and other osmoprotectants (Ozga et al., 2017).

These responses work in concert to protect the photosynthetic apparatus, reduce oxidative damage, and ensure survival and productivity in hostile environments.

Practically, these physiological traits contribute to greater yield stability in low-input farming systems, where water stress is common and external inputs (e.g., irrigation, fertiliser) are limited. Their integration into breeding programmes offers the potential to develop drought-resilient cultivars without compromising yield. Furthermore, a better understanding of these mechanisms in underutilised legumes could guide management practices such as timing of sowing, crop spacing, and intercropping design to optimise water use and support the resilience goals of climate-smart agriculture.

2.4.3 Biological Nitrogen Fixation

While biological nitrogen fixation (BNF) is a well-known trait across nearly all legume species, what is often more agronomically relevant is the degree of host selectivity and symbiotic efficiency with rhizobial strains. This becomes particularly important in smallholder contexts, where access to commercial inoculants is limited and synthetic fertilisers are often unaffordable (Masso et al., 2016). In such low-input systems, crops that can form effective, spontaneous associations with native rhizobia are especially valuable.

Among the underutilised legumes examined, pigeon pea stands out as the most beneficial option for smallholder farmers. It readily forms symbioses with indigenous rhizobia in many African soils and can fix between 40 and 60 kg N ha^{-1} through a combination of nodulation and nitrogen-rich leaf litter (Ansari and Mahmood, 2017, Kizito, 2018). Its reliable nitrogen fixation without the need for inoculation makes it a practical and accessible solution for nutrient-poor environments.

Tepary bean also shows strong potential for nitrogen fixation. It forms symbiosis with *Rhizobium* sp. strain R3254 and has been reported to fix up to 260 kg N ha^{-1} under optimal conditions (Ullah, 2010). However, such rates are rarely realized in smallholder field environments. More conservative field-based estimates place fixation at 20–50 kg N ha^{-1}, particularly under arid and semi-arid conditions where the crop is typically grown (Singh et al., 2024). While tepary bean has demonstrated the ability to nodulate without inoculation in some soils, its effectiveness is still influenced by the availability of compatible native rhizobia. Further field-based research is needed to confirm its consistency across different agroecological zones and inform targeted inoculation strategies.

In contrast, Bambara groundnut shows greater variability in its symbiotic performance. It is known to associate with indigenous *Bradyrhizobium* strains, but nodulation efficiency depends heavily on genotype and environmental conditions (Bitire et al., 2022, Mayes et al., 2019) . Reported nitrogen fixation rates range up to 28.42 kg N ha^{-1} (Fwanyanga et al., 2022), but often fall short without inoculation. As such, Bambara is less suited to spontaneous nitrogen fixation in low-input settings and would benefit from targeted inoculation strategies or breeding efforts to improve its BNF efficiency.

For smallholder farmers, the implications are clear: understanding whether a legume requires inoculation to achieve meaningful BNF is critical for its successful adoption. Of the three crops discussed, pigeon pea offers the most consistent benefit, followed by tepary bean, while Bambara groundnut currently presents more limitations unless supported by interventions. Promoting legumes with spontaneous BNF capacity can reduce fertiliser costs, improve soil health, and contribute to more sustainable and climate-resilient farming systems.

2.4.4 Early Maturity and Cropping Flexibility

In rainfed and drought-prone agroecosystems, early maturity and cropping flexibility are essential traits that contribute to both productivity and risk reduction. These traits allow farmers to align crop cycles with short or shifting rainfall patterns, support crop diversification, and reduce exposure to terminal drought. Underutilised legumes such as tepary bean, pigeon pea, and Bambara groundnut exhibit varying degrees of maturity and photoperiod responsiveness, which influences their suitability for different climates and cropping systems.

Tepary bean is among the most notable for its short growth cycle, typically reaching maturity within 60–90 days (Ghadimian et al., 2021). This rapid lifecycle enables farmers to take advantage of brief rainy seasons or grow the crop between major planting windows (Mwale et al., 2020). Its ability to thrive under high temperatures and minimal water input makes it especially useful in short-season cultivation, where conventional legumes often fail. This maturity profile supports its use in relay planting, post-harvest rotations, and intercropping arrangements with cereals in dryland zones.

Pigeon pea offers a contrasting example, with a wide range of maturity durations—from early-maturing improved cultivars (90–145 days) to long-duration landraces that can take up to 300 days to reach physiological maturity (Hluyako et al., 2017, Varshney et al., 2010). This diversity is largely influenced by photoperiod sensitivity and agroecological conditions. Early-maturing genotypes, developed by institutions such as ICRISAT, are particularly valuable in regions with short growing seasons or where pigeon pea is used in double cropping systems. These cultivars allow farmers to plant a second crop such as wheat, barley, mustard, or chickpea after harvest, improving land-use efficiency and food security (Nandhini et al., 2015). In contrast, long-duration types are better suited for monoculture systems in areas where land pressure is lower and rainfall is more evenly distributed throughout the year.

Bambara groundnut, however, presents a unique challenge. It is predominantly grown as genetically heterogeneous landraces, many of which exhibit photoperiod sensitivity, particularly affecting pod development and seed filling rather than flowering. While flowering in most genotypes occurs regardless of daylength, pod set is significantly delayed or suppressed under long photoperiods exceeding 14 hours (Mubaiwa et al., 2018). This can result in asynchronous maturity, uneven harvests, and poor grain quality, particularly in regions farther from the equator (Mayes et al., 2019). Moreover, long daylengths promote vegetative growth at the expense of reproductive development, likely due to altered assimilate partitioning (Gerrano et al., 2021). These physiological constraints limit Bambara groundnut's geographic adaptability and its incorporation into intensified cropping systems.

To address these limitations, targeted breeding for photoperiod-insensitive and short-duration Bambara varieties is urgently needed. Such cultivars would enable synchronised maturity, shorten the harvest window, and allow for double cropping in regions with limited or erratic rainfall. Optimising maturity profiles and photoperiod responses in these underutilised legumes can help farmers better align planting decisions with climate variability, reduce harvest risk, and enhance system resilience—making these crops key tools in the implementation of climate-smart agriculture across sub-Saharan Africa.

2.4.5 Seed Priming Response

In low input, rainfed farming systems, rapid and uniform crop establishment is essential for productivity and climate resilience. One technique that has shown promise in enhancing early-stage performance is seed priming, a pre-sowing treatment in which seeds are partially hydrated to activate metabolic processes without initiating radicle emergence (Bhowmick et al., 2013). Among the various approaches, hydro-priming is the simplest and most accessible typically involves soaking seeds in clean water for a period of hours, followed by re-drying prior to planting (Ghassemi-Golezani, 2008). This low-cost, farmer-friendly intervention can significantly improve germination rate, seedling vigour, and emergence uniformity, especially under erratic or delayed rainfall conditions (Chisa et al., 2025).

For smallholder farmers, who often contend with low seed vigour, hard seed coats, and unpredictable field conditions, priming provides a practical means to overcome establishment failures (Mandizvo and Odindo, 2019; Hluyako et al., 2017). Among the legumes reviewed, Bambara groundnut has shown the most consistent and substantial response to hydro-priming. In a study by Legwaila et al. (2013), 24-hour priming reduced the coefficient of variation (CV) for emergence time by 30% and improved biomass accumulation. More recent work by Chisa et al. (2025) reported a 50% reduction in days to emergence and a 60% increase in total plant dry mass after 36-hour priming, compared to non-primed controls. Such results suggest that priming helps synchronise seedling emergence, an important trait for labour-efficient crop management, particularly where timely weeding and field operations are constrained.

In contrast, tepary bean and pigeon pea generally exhibit strong emergence under favourable conditions, likely reflecting evolutionary selection for survival in arid zones. However, limited field-based evidence exists on the benefits of priming under stressful or variable environments. A study by Sajjan et al. (2017) found modest gains in seedling vigour, with pigeon pea exhibiting physiological changes including enhanced mobilisation of storage proteins like 11S globulin. These findings highlight the genotype-specific and context-dependent nature of priming responses, reinforcing the need for tailored protocols.

While some advantages of seed priming, such as emergence uniformity, may seem relevant to commercial farming, in practice, formal systems rarely require such interventions. This is due to their reliance on high-vigour, genetically improved seed lines optimised for uniform germination (Afzal et al., 2020, Zhang et al., 2015). Additionally, 24–36-hour soaking and drying period may introduce delays incompatible with high-throughput planting schedules in mechanised systems (Jarrar et al., 2023).

Instead, the primary value of seed priming lies in smallholder contexts, where resource limitations and climate variability hinder consistent crop establishment. In these settings, priming offers a cost-effective and scalable tool for improving stand uniformity, reducing replanting, and enhancing yield reliability, particularly in dryland agroecosystems (Devika et al., 2021, Waqas et al., 2019). For further research, the development of species- and genotype-specific priming protocols, coupled with integration into extension programmes, is essential for translating controlled-environment successes into on-farm impact.

Despite the growing evidence on the benefits of seed priming across legume species, limited empirical work exists on genotype-specific hydro-priming responses in Bambara groundnut, particularly concerning early establishment under water stress. Understanding these differential responses is critical for identifying trait-based mechanisms that confer improved germination, emergence, and early vigour under drought-prone conditions. Future studies should therefore focus on controlled and field-based evaluations across diverse landraces to develop optimised, context-specific priming protocols that enhance the resilience and productivity of Bambara groundnut in dryland systems.

2.5. Research and Policy Gaps Hindering the Scaling-up of Underutilised Legumes in CSA

Despite their alignment with climate-smart agriculture (CSA) principles, underutilised legumes such as Bambara groundnut, tepary bean, and pigeon pea remain marginal in formal agricultural systems across sub-Saharan Africa. Their limited adoption is shaped by a combination of technical constraints, including gaps in breeding, agronomy, and seed systems and institutional challenges such as weak policy integration, minimal extension support, and underdeveloped markets (Garbero et al., 2018).

Although progress has been made in breeding and characterising traits such as drought tolerance, early maturity, and nutritional content, research investment in these crops remains significantly lower than in major staples (Ghimire et al., 2022). Many varieties developed by public research institutions fail to reach farmers due to fragmented dissemination pathways, lack of commercialisation incentives, and limited seed system capacity. Akpo et al. (2021) reports that a percentage of farmers (80–90%), have no access to recently released and high-yielding varieties prove the failure of various seed delivery models implemented. Advances in modern genomics and participatory breeding offer new opportunities (Mwale et al., 2020), but require strategic investment to bridge genotype–environment gaps and accelerate domestication.

Agronomic research is also limited, with few context-specific recommendations to other regions. Seed priming of legumes such as Bambara groundnut and pigeon pea, though promising, has been widely tested in controlled settings (Ghassemi-Golezani, 2008, Sajjan et al., 2017, Marthandan et al., 2020) and remains under-evaluated across diverse environments and landraces. Farmer-participatory trials, genotype–environment assessments, and adaptive agronomic strategies are needed to develop practical, scalable solutions.

Beyond research, systemic barriers continue to restrict uptake. Extension services are under-resourced and often unfamiliar with underutilised legumes, leading to low awareness and adoption among farmers (Akpo et al., 2021). Improved varieties may be included in seed catalogues for research purposes but are rarely available in agro-dealer networks for broader distribution (Porch et al., 2024). Smallholders continue to rely on unimproved landraces that are poorly adapted to climate variability and offer limited economic returns (Jiri and Mafongoya, 2016),

Policy and institutional disconnects further impede impact. While these crops are referenced in CSA strategies and development plans, they remain largely absent from formal procurement systems, seed subsidy schemes, and nutrition-sensitive programming. Research institutions often lack the mandate or resources to ensure the long-term scaling of innovations beyond pilot projects.

Consumer awareness is another constraint. Underutilised legumes are often stigmatised as "poor people's food" and rarely feature in urban diets or school feeding programmes (Knez et al., 2023, Olanrewaju et al., 2022). Meanwhile, industrial legumes such as soybeans benefit from substantial investment, visibility, and policy support (Siddique et al., 2012, de Visser et al., 2014), perpetuating dietary dependence on a narrow range of staples.

Addressing these barriers requires a coordinated, whole-of-system approach. Researchers must work alongside seed producers and agro-enterprises to commercialise climate-resilient varieties. Governments should integrate underutilised legumes into national CSA investment plans, seed strategies, and public procurement schemes (Makate, 2019). Donors and policymakers are increasingly recognising the role of SMEs and private-sector actors in scaling inclusive innovation, with new frameworks supporting sustainable development and smallholder empowerment(Chavez-Tafur et al., 2020, Pouw et al., 2019). Extension systems must also be capacitated to support both cultivation and consumption, particularly in nutrition-sensitive contexts.

Table 2.0.2 summarises the key research and policy gaps hindering the mainstreaming of underutilised legumes and outlines strategic priorities aligned with the CSA pillars of productivity, resilience, and mitigation. By addressing both technical and institutional constraints, these crops can play a transformative role in realising Sustainable Development Goals 2 (Zero Hunger), 3 (Health and Well-being), 12 (Responsible Consumption and Production), and 13 (Climate Action). While not a panacea, mainstreaming underutilised legumes into CSA frameworks offers a scalable and evidence-based pathway to resilient, inclusive, and nutritious food systems in Africa.

Table 2.0.2: Key research and policy gaps limiting uptake of underutilized legumes and strategic CSA priorities

Identified Gap	Description	Strategic Priority	CSA Pillar Addressed
Genotypic characterization & breeding	Limited genomic and phenotypic data on traits like drought tolerance, maturity, and nutrition	Invest in multi-trait breeding across agroecological zones using modern genomic tools	Productivity & Resilience
Context-specific agronomy evaluations	Limited region-specific agronomic guidelines for low-input smallholder systems	Conduct farmer-participatory trials and adaptive agronomic research	Productivity & Resilience
Seed priming field validation	Most studies are conducted in controlled conditions; lack of real-world validation	Evaluate priming techniques under diverse field conditions with different landraces	Resilience
Weak extension & farmer knowledge	Insufficient farmer training and access to extension services	Incorporate legumes into extension materials and provide targeted training programs	Productivity
Socio-cultural barriers & limited awareness	Perception as 'poor man's food'; limited consumer demand and cooking knowledge	Conduct perception studies and design nutrition and awareness campaigns	Productivity
Policy & institutional disconnect	Limited coordination between research, policy, and commercial pathways	Develop whole-of-system strategies linking research outputs to market and policy actions	All three (Productivity, Resilience, Mitigation)
Underdeveloped seed & market systems	Limited access to improved seed, weak processing infrastructure, and low market incentives	Strengthening seed systems, support agro-processing, and incentivize private sector investment	Productivity & Economic Viability

2.6. Conclusion

The review highlighted significant knowledge gaps limiting the integration of underutilised legumes into climate-smart agriculture (CSA) systems in sub-Saharan Africa. Despite their demonstrated potential for productivity, resilience, and mitigation through traits such as drought tolerance, nitrogen fixation, and adaptability to marginal environments, crops like Bambara groundnut, tepary bean, and pigeon pea remain under-researched and underutilised.

The first gap identified relates to limited understanding of root system architecture and its contribution to drought adaptation, justifying Objective 1, which focuses on the phenotypic characterisation of root traits under contrasting water regimes. The second gap concerns inconsistent field establishment and poor seedling performance, supporting Objective 2, which investigates the physiological and structural determinants of seed coat traits and their influence on germination. The third gap involves a lack of low-cost management interventions to improve establishment in rainfed systems, underpinning Objective 3, which examines the role of seed priming as a farmer-friendly technique to enhance vigour and drought resilience.

Addressing these gaps through targeted experimentation provides a pathway to reposition underutilised legumes as integral to resilient and nutrition-sensitive food systems. The combined insights from the three objectives contribute to evidence-based strategies for trait improvement, breeding prioritisation, and sustainable management, advancing the realisation of CSA goals and related Sustainable Development Goals (SDGs 2, 3, 12, and 13).

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CHAPTER 3: PHENOTYPING ROOT TRAITS FOR DROUGHT TOLERANCE IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA (L.) VERDC.)*

Abstract

Drought stress poses a significant challenge to food security in sub-Saharan Africa, particularly for smallholder farmers in dryland systems. Bambara groundnut (*(Vigna subterranea (L.) Verdc.)*), an underutilised legume with inherent drought tolerance, remains underexplored in terms of its root system traits. This greenhouse study investigated the early root and shoot responses of six Bambara groundnut genotypes, under well-watered (100% field capacity) and water-stressed (50% field capacity) conditions using rhizotron-based phenotyping. Significant genotypic differences ($p < 0.01$) were observed in root traits such as root system depth (RSD: 11.0–19.9 cm), root shoot width (RSW: 6.96–12.2 cm), and root dry mass (RDM: 0.42–1.27 g). ARC exhibited a strong drought-avoidance strategy, increasing RSD from 12.2 to 19.9 cm and RDM from 0.42 to 1.16 g under stress. Tiga Nicuru DIP-C-F7471 showed adaptive plasticity, maintaining deeper roots (11.0–14.5 cm) and high CHA and RSR values, despite a reduction in RDM, suggesting a resource-conserving strategy. Principal Component Analysis (PCA) captured 93.6% of the total variability among genotypes. Root traits, particularly total root length (TRL), convex hull area (CHA), root system width (RSW), and root dry mass (RDM) were the main contributors to genotype differentiation. Strong positive correlations ($r = 0.88$–0.97) between root and shoot traits suggest that genotypes with more developed root systems also supported greater shoot growth, highlighting the coordinated response of above- and below-ground traits under drought stress. These findings offer valuable targets for breeding and highlight the value of rhizotron-based screening for root trait selection. Future field validation and full-season studies are recommended to confirm the relevance for improving yield stability in dryland agriculture.

Keywords: Water scarcity, root system architecture, legumes, climate-smart agriculture, underutilized crops

3.1. Introduction

Crops frequently encounter a wide range of environmental stresses that jeopardise their survival, growth, and reproduction in natural ecosystems , while also negatively impacting crop yield and quality in agricultural farming systems (Maqbool et al., 2022, FAO, 2020). Climate change, particularly drought and erratic rainfall, are examples of these stressors and continues to threaten food and nutritional security across sub-Saharan Africa (Bazylevych and Kupalova, 2014).

Plants adopt three main strategies to cope with drought: avoidance, escape, and tolerance (Fang et al., 2017, Kooyers, 2015). Drought avoidance involves morphological and physiological changes such as fewer stomata, smaller leaves, deeper roots, waxy cuticles, and leaf rolling to minimise water loss and osmotic stress (Lee and Suh, 2013, Liu et al., 2017). Drought escape refers to rapid life cycle completion through early flowering, enhanced photosynthesis, higher nitrogen levels, and fast growth, allowing the plant to reproduce before drought onset (Kooyers, 2015, Marthandan et al., 2020). While long crop cycles are ideal under normal conditions for maximum light capture, they reduce fitness under drought due to early soil moisture depletion (Tardieu et al., 2018, Varshney et al., 2021). Drought-tolerant plants accumulate osmolytes like proline and glycine, which activate the phenylpropanoid pathway, boosting lignin production and phytoalexin synthesis to stabilise membranes and resist stress (Sharma et al., 2019, Nadeem et al., 2019, Sheoran et al., 2022).

Addressing water scarcity due to drought in agriculture is crucial for attaining Zero Hunger, one of the 17 Sustainable Development Goals outlined in the 2030 Agenda FAOSTAT (2020). Therefore, it is essential to develop high-yielding crops capable of thriving under limited water availability, especially in dryland farming systems, to support global food security (Huang et al., 2017). Although considerable progress has been made in understanding how above-ground plant parts adapt to climate change, the study of root system responses has remained relatively overlooked

The root system is fundamental to the growth of terrestrial plants, serving as an anchor in the soil while also acting as the primary pathway for water and nutrient uptake from the surrounding environment (Kou et al., 2022, Gupta et al., 2020). Root system architecture (RSA), the system that describes how roots grow, branch, and spread in the soil (Mateva et al., 2022). Traits such as root depth, lateral spread, and root-to-shoot allocation can influence a plant's ability to survive and perform during water shortages (Kalra et al., 2024). Yet, root traits are often neglected in crop improvement research because they are harder to observe and measure than above-ground traits like plant height or yield (Chen et al., 2017). This is especially true for underutilised crops like Bambara groundnut, where limited data on root development slows progress in identifying and breeding climate-resilient varieties.

Bambara groundnut (*Vigna subterranea* (L.) Verdc.) is highly drought-tolerant, nutritionally rich, and well-suited to low-input, smallholder farming systems (Mayes et al., 2019). However, despite its promise, Bambara groundnut remains under-researched, especially when it comes to understanding how its roots contribute to drought adaptation.

Some studies suggest that Bambara groundnut has a wide range of root growth patterns that differ between genotypes. Mayes et al. (2019) found that the agroecological environment in which Bambara groundnut is grown, such as whether it originates from a dry or wet region, can influence root phenotypic variation. This highlights the importance of phenotyping root traits under water-limited conditions, as root architecture plays a critical role in drought adaptation. Given the increasing frequency of drought events, identifying landraces with superior root systems capable of accessing deeper or more persistent water sources is essential for improving resilience (Polania et al., 2017). Variation in drought tolerance has been observed among Bambara groundnut landraces (Mateva et al., 2022), underscoring the potential for selecting genotypes with enhanced performance under water stress.

Studying root traits, however, presents several methodological and logistical challenges that have historically limited progress in understanding below-ground adaptations. Root systems are complex and highly dynamic, making them difficult to measure without disrupting their natural growth environment (Chen et al., 2017). Conventional methods often destructive, labour-intensive, and time-consuming, providing only a snapshot of the root system at a given point rather than capturing its temporal development (Lynch, 2019). Moreover, field-based root studies are constrained by soil heterogeneity, environmental variability, and the difficulty of accessing deeper root layers, all of which complicate data interpretation (Maqbool et al., 2022). These limitations have contributed to a significant knowledge gap in root phenotyping for many underutilised crops, including Bambara groundnut, where consistent and non-destructive methods for evaluating root system architecture (RSA) remain underdeveloped.

To address these challenges, rhizotron systems offer an effective approach. Rhizotrons are soil-filled, transparent-sided boxes or chambers that allow researchers to observe and measure root growth over time without disturbing the plant (Mandizvo et al., 2022). Unlike hydroponic systems or traditional destructive sampling methods, rhizotrons provide a more natural growing environment while still enabling detailed observation of root traits such as depth, angle, spread, and density. This makes them especially valuable for screening early-stage root development under different environmental conditions, such as water stress. Studies in other legumes (e.g. Mateva et al., 2020; Adu et al., 2022) have shown that structures like rhizotron are reliable for capturing fine differences in RSA that are relevant for drought adaptation.

This study aims to address current knowledge gaps by assessing the root system architecture and early shoot growth of six Bambara groundnut genotypes, under both well-watered and water-stressed conditions using a rhizotron setup. The goal is to understand how these genotypes differ in their root development and allocation patterns in response to water availability. Identifying these differences is important for selecting Bambara groundnut varieties that are better suited to drought-prone areas. In the context of the climate crisis, this information can support smallholder farmers by improving access to crop varieties that perform better under dry conditions, while also helping plant breeders develop more resilient, locally adapted legume cultivars.

3.2. Materials and Methods

3.2.1 Plant material and experimental design

This experiment was conducted at the Controlled Environment Facility of the University of KwaZulu-Natal, Pietermaritzburg, Pietermaritzburg, South Africa (29°37′37.5″ S; 30°24′10.4″ E). Six Bambara groundnut (Table 3.0.1) were selected based on prior agronomic evaluation and visual distinction. Seeds were obtained from the University of KwaZulu-Natal's Bambara groundnut germplasm collection. To ensure uniform germination and minimise variation due to environmental history, seeds were harvested during the same growing season and stored under controlled ambient conditions until use.

A completely randomised design (CRD) was used, arranged in a 2 × 6 factorial layout, comprising two water regimes (well-watered and water-stressed) and six genotypes. Each treatment combination was replicated three times, totalling 36 experimental units. To minimise spatial variation due to light, airflow, or temperature gradients in the greenhouse, rhizotron units were rotated every three days throughout the experimental period.

Table 3.0.1: List of selected Bambara groundnut genotypes

Genotype	Colour	Origin
ARC	Brown	South Africa
Tiga nicuru/DipC -F7471	Red	Mali
Tiga nicuru/DipC -F7445	Purple	Mali
NW	Cream (white)	Namibia
Tiga nicuru/DipC -F7472	Brown (light)	Mali
DIP-C	Cream	Botswana

3.3.2. Greenhouse conditions and growth medium

The experiment was conducted under controlled greenhouse conditions at the Controlled Environment Facility (CEF), University of KwaZulu-Natal, Pietermaritzburg, South Africa (29°37'37.5"S, 30°24'10.4"E). The mean air temperature was maintained at 25 ± 2 °C, with a relative humidity of 60 ± 3%, and a natural light photoperiod was supplemented to maintain 12 h of daylight.

The growth medium comprised a mixture of Gromor Potting Mix (30 dm^3) and coarse sand in a 3:1 (v/v) ratio was used as the growth substrate. This combination was selected following preliminary testing for optimal texture, drainage, and water-holding capacity, ensuring sufficient aeration while retaining enough moisture to simulate realistic soil conditions under both water-stressed and non-stressed treatments. The potting mix was sieved through a 2 mm mesh to remove debris, then sterilised at 105 °C for 24 h to eliminate microbial contaminants. The substrate was thoroughly homogenised and packed uniformly into each rhizotron to ensure consistent rooting conditions across treatments.

3.2.3 Rhizotron construction and setup

Rhizotron units were constructed following the design outlined by Mandizvo et al. (2022), with minor modifications tailored to Bambara groundnut. Transparent acrylic sheets (3 mm thickness) were cut into rectangular panels measuring 30 cm in height, 20 cm in width, and with an internal depth of 3 cm. Plastic tubing (2 cm diameter) was cut to match the height and depth of the acrylic panels and served as lateral supports within the rhizotron structure (Figure 3.1).

Figure 3.0.1: Rhizotron structure (THIS IS A NEW IMAGE)

To ensure precision during assembly, all components were aligned and clamped using a Grip GV9365 Bench Vice (100 mm) before drilling pilot holes. The panels were then secured using Keystone Electronic machine screws (2.34 × 8.69 mm). Each assembled rhizotron enclosed approximately 1.8×10^{-3} m^3 of soil and had a final weight of 0.95 ± 0.04 kg.

During plant growth, each rhizotron was positioned at a 45° angle to encourage root development along the transparent surface, facilitating non-destructive visualisation. To exclude light and simulate belowground soil conditions, the transparent face of each rhizotron was covered with black polyethylene plastic throughout the experimental period.

3.2.4 Watering treatments

Watering treatments were initiated at 10 days after sowing (DAS), once all seedlings had germinated and were visibly established. Two distinct soil moisture regimes were applied:

Well-watered (WW): Soil moisture maintained at 100% field capacity (FC)

Water-stressed (WS): Soil moisture maintained at 50% field capacity

Field capacity was determined gravimetrically by saturating a representative soil sample and allowing it to drain freely under gravity for 48 hours. The difference between the saturated and oven-dried weights was used to calculate the water content at field capacity. Based on the rhizotron soil mass of 950 g per unit, the estimated water volume required to reach 100% FC was 145 mL. Accordingly, the water-stressed treatment received 70 mL to represent 50% FC.

The selection of 50% FC was guided by prior drought-screening protocols for legumes (Afonso et al., 2025), which identified this threshold as sufficient to impose moderate but physiologically meaningful stress without inducing plant mortality. Preliminary calibration trials further confirmed that this level produced consistent reductions in growth and soil moisture content while maintaining plant viability throughout the experiment

Rhizotrons were weighed daily using a digital scale, and water was replenished as needed using a graduated syringe to return each unit to its target weight. This method ensured consistent moisture levels per treatment while avoiding disturbance of the soil or root system.

3.2.5 Data collection and image acquisition

Plants were harvested at 35 days after sowing (DAS) for data collection (Table 3.0.2). Shoots were cut at the soil line, and roots were carefully excavated for measurement. All harvested plant material was oven-dried at 60 °C for 72 hours to determine dry mass.

Root growth was monitored through time-series image acquisition using a fixed camera setup. A digital camera (Apple iPhone 12, 16 MP, Apple Inc., California, United States) was mounted at a consistent distance of 80 cm from the rhizotron. Images were captured daily from both lateral sides of the rhizotron between 8 and 35 days after planting (DAP). The camera settings included a 4:3 resolution ratio, assistive grid enabled, a 3-second timer, and wide-angle mode (26 mm). Images were saved in raw format at a resolution of 3024 × 4032 pixels using the 12 MP wide camera.

Leaf area was measured using the Easy Leaf Area smartphone application (Heaslon, University of California, California, USA)

Table 3.0.2: Summary of the traits, definitions, methods and units

Trait	Full name	Unit	Description
RSD	Root System Depth	cm	Vertical extent of the root system; primary measure of rooting depth
RSW	Root System Width	cm	Horizontal spread of the root system
CHA	Convex Hull Area	cm^2	2D area occupied by the root system; approximated as a triangle (½ × RSW × RSD)
TRV	Total Root Volume	cm^3	Estimated root system volume; calculated using a conical model
SRA	Seminal Root Angle	degrees (°)	Angle between outermost seminal roots; derived from RSW and FSRL geometry
SL	Shoot Length	cm	Length from base to tip of the shoot; reduced under water stress
LA	Leaf Area	cm^2	Total leaf surface area; calculated from SL using empirical model
SDM	Shoot Dry Mass	g	Estimated dry mass of the shoot; based on LA
RDM	Root Dry Mass	g	Estimated dry mass of roots; based on TRV
RSR	Root-to-Shoot Ratio	ratio	Alternate expression of RSM; RDM divided by SDM
RMR	Root Mass Ratio	unitless	Proportion of total biomass allocated to roots: RDM / (RDM + SDM)
SMR	Shoot Mass Ratio	unitless	Proportion of total biomass allocated to shoots: SDM / (RDM + SDM)

3.2.6. Image Analysis

Root system 2-D images captured from the rhizotron were processed using RootSnap software (Version 1.3.2.25, CID Bio-Science Inc., Camas, WA, USA). The analysis was carried out primarily in automatic mode, with manual adjustments applied where necessary (Figure 3.0.2). A Microsoft Surface tablet, along with a Surface Pro 4 stylus, was used to manually trace and refine root outlines during analysis. Key architectural traits of the root system (as listed in Table 1) were extracted from these images using the semi-automated RootSnap software.

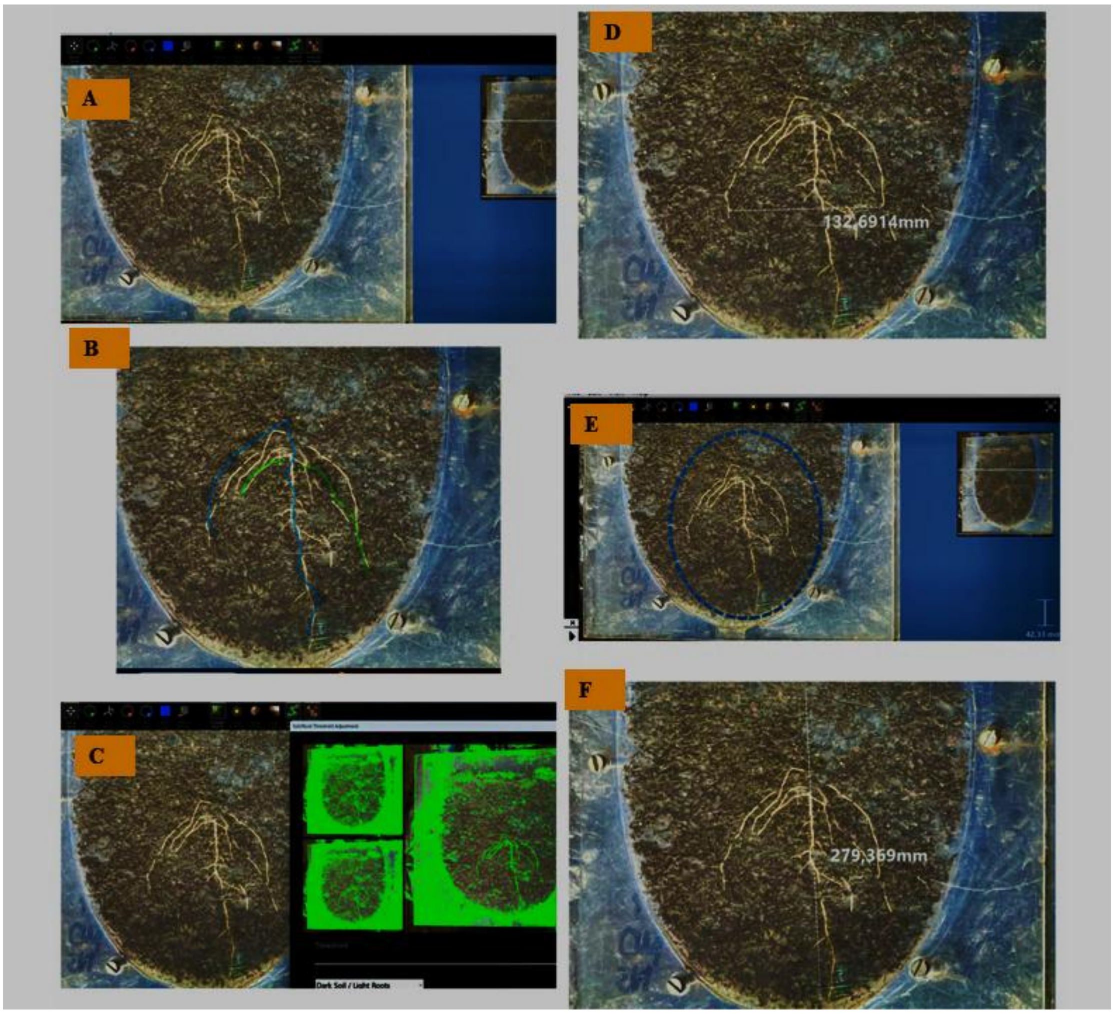


Figure 3.0.2: Illustration of how RootSnap software was used to analyse and collect data from captured root images: (A) root image in raw format imported from local storage to RootSnap; (B) tracing the root using Microsoft Surface Pro 4 stylus to measure total root length; (C) automated digital image analysis mode;(D) measurement of root system depth; (E) measurement of root convex hull area; (F) measurement of root system width.

3.2.6. Statistical Analysis

All data were analysed using a two-way Analysis of Variance (ANOVA) in Genstat® 22nd Edition (VSN International Ltd., Hemel Hempstead, UK) to assess the main effects of genotype, water regime, and their interaction on each measured root trait. The ANOVA was conducted under a factorial design, and treatment means were compared at a significance level of $p < 0.05$. When significant differences were detected, mean separation was performed using Duncan's Multiple Range Test (DMRT) to identify statistically distinct groups. Mean values followed by the same letter were not significantly different, whereas those with different letters indicated significant differences. Before performing the ANOVA, data were tested for normality using the Shapiro–Wilk test and for homogeneity of variances using Levene's test to ensure compliance with ANOVA assumptions.

To explore multivariate patterns and trait interrelationships, Principal Component Analysis (PCA) was conducted using XLSTAT 2025 (Addinsoft, Paris, France) to identify key traits contributing to genotype differentiation under different water regimes. Additionally, Pearson's correlation analysis was performed using OriginLab® 2023 (OriginLab Corporation, Northampton, MA, USA) to assess relationships among root and shoot traits.

3.3. Results

3.3.1 Genotypic, irrigation, and interaction effects on root and shoot traits

Analysis of variance (Table 3.0.3) shows significant genotypic effects ($p < 0.01$) for several key root traits, including convex hull area (CHA), root branch count (RBC), root system depth (RSD), root system width (RSW), and total root length (TRL), highlighting substantial variability in root architectural traits among Bambara groundnut landraces. Genotypes also differed significantly ($p < 0.05$) in shoot length (SL) and leaf area (LA), reflecting above-ground morphological diversity. In contrast, genotype did not significantly influence biomass traits such as root dry mass (RDM), shoot dry mass (SDM), root mass ratio (RMR), shoot mass ratio (SMR), or root-shoot ratio (RSR), suggesting that dry matter partitioning was more stable across landraces.

Significant genotype × irrigation interactions (Figure 3.0.3) were detected for CHA ($p < 0.01$), RBC ($p < 0.01$), RDM ($p < 0.01$), RSD ($p < 0.05$), RSR ($p < 0.01$), RSW ($p < 0.01$), and TRL ($p < 0.05$), indicating that genotypic responses to water availability varied depending on the trait. Under WS conditions, the genotype Tiga Nicuru DIP-C-F7471 consistently maintained higher values for CHA, RDM, and RSR, while DIP-C and TIGD showed notable declines, suggesting contrasting drought responses. RSD increased in several genotypes under WS, particularly ARC and Tiga Nicuru DIP-C-F7471, highlighting their potential for improved.

Table 3.0.3: Analysis of variance showing mean squares and significance levels for root and shoot traits of Bambara groundnut landraces under two water regimes

Source of variation	**d.f**	**CHA**	**LA**	**RBC**	**RDM**	**RMR**	**RSD**	**RSR**	**RSW**	**SDM**	**SL**	**SMR**	**TRV**	**TRL**
Genotype (G)	5	28801**	1071.4**	58.778**	0.447**	0.003^{NS}	56.805**	0.034^{NS}	23.243**	0.283^{NS}	38.312**	0.003^{NS}	0.0002**	346.79**
Irrigation (I)	1	59278 ^{NS}	5490.8**	16.000^{NS}	0.253^{NS}	0.197**	610.337**	3.789**	54.072**	2.430**	180.231 **	0.197**	0.001**	428.08**
G × I	24	16732 **	99.3 ^{NS}	88.267**	1.105**	0.004^{NS}	17.680*	0.217**	16.928**	0.170^{NS}	0.485^{NS}	0.004^{NS}	0.0006^{NS}	83.05*
Residual	35	2263^{NS}	174.7 ^{NS}	6.167^{NS}	0.037^{NS}	0.0014^{NS}	4.146^{NS}	0.017^{NS}	2.557^{NS}	0.124^{NS}	5.646^{NS}	0.001^{NS}	0.0003 ^{NS}	21.85^{NS}

d.f; degrees of freedom, NS= not significant. *= $P < 0.05$; **= $P < 0.01$. convex hull area (CHA), shoot length (SL), total root length (TRL), root branch count (RBC), root system depth (RSD), leaf area (LA), root dry mass (RDM), shoot dry mass (SDM), whole plant dry mass (WPDM), root shoot ratio (RSR), shoot mass ratio (SMR), total root volume (TRV) and root mass ratio (RMR)

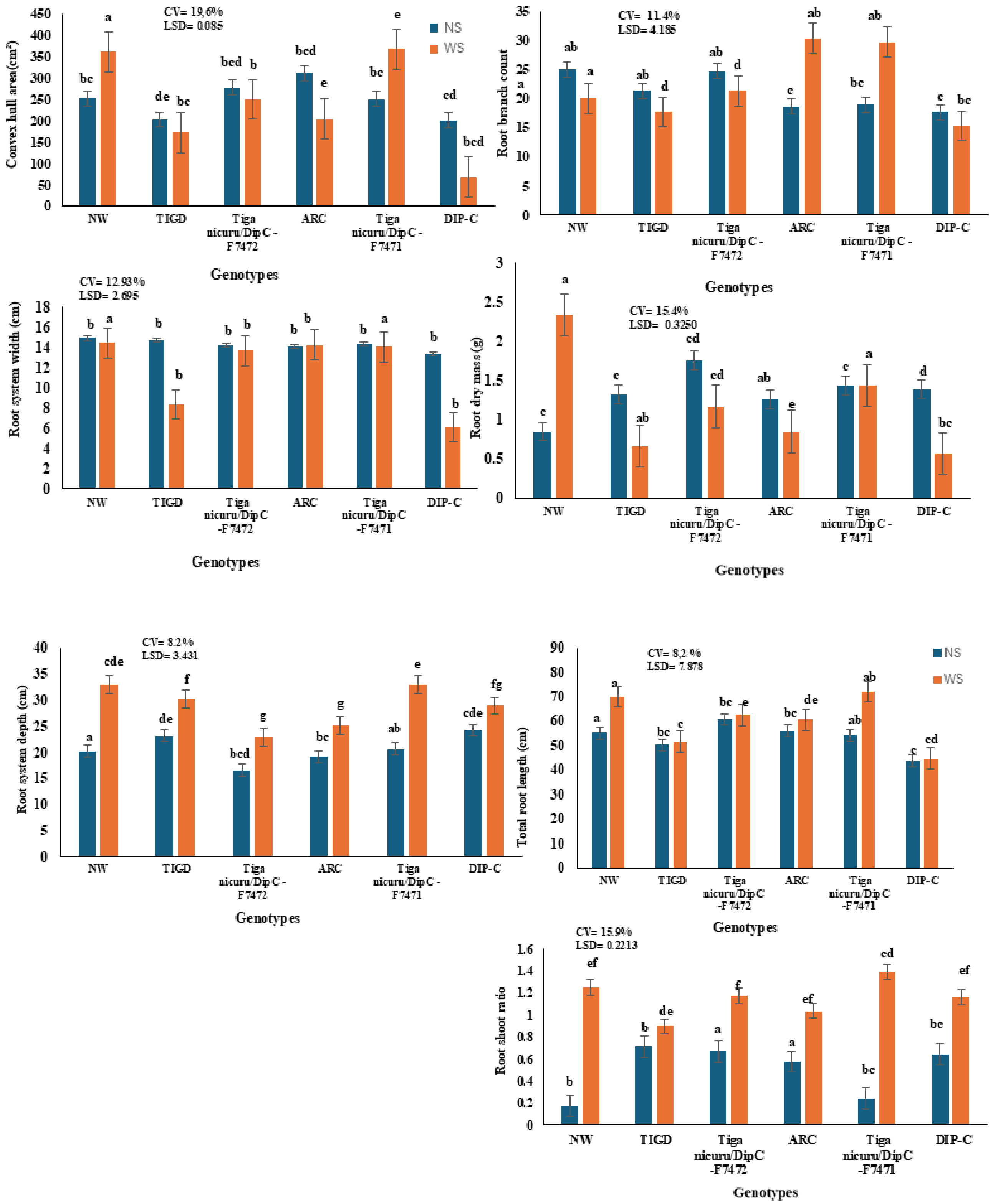


Figure 3.0.3: Comparative analysis of root morphological traits in six Bambara groundnut genotypes under no-stress (NS) and water-stressed (WS) conditions

Traits measured include convex hull area (cm^2), root branch count, total root length (cm), root system width (cm), root dry mass (g), root-shoot ratio, and root system depth (cm). Plants were grown under two irrigation treatments: non-stressed (NS) and water-stressed (WS). Bars represent means ± standard error (n = 3). Different lowercase letters above bars indicate significant differences among genotype × irrigation combinations based on LSD at $p \leq 0.05$. Coefficient of variation (CV%) and least significant difference (LSD) values are indicated for each trait.

3.3.2 Principal component analysis (PCA) of root and shoot traits

PCA was conducted to identify the major sources of variation among root and shoot traits in Bambara groundnut under contrasting water regimes. The first two principal components (PC1 and PC2) accounted for a cumulative 93.63% of the total variation, with PC1 explaining 72.33% and PC2 explaining 21.29%. PC1 (Table 3.0.4) was positively associated with key root architectural traits, including convex hull area (CHA, loading = 0.985), total root length (TRL, 0.991), root system depth (RSD, 0.982), root system width (RSW, 0.992), and root branch count (RBC, 0.920), as well as above-ground traits such as shoot length (SL, 0.920) and shoot dry mass (SDM, 0.855). This indicates that PC1 captures overall plant structural vigour and root system expansion. Notably, trait co-variation was evident, as genotypes exhibiting high RSW also tended to show elevated values for TRL and RDM, highlighting the functional linkage between horizontal spread, root elongation, and biomass accumulation under water stress.

PC2 (Table 3.0.4) was defined primarily by traits related to biomass allocation. Root-shoot ratio (RSR, loading = 0.836) and root mass ratio (RMR, 0.774) contributed positively, while shoot mass ratio (SMR, –0.774) loaded negatively, indicating a trade-off between shoot and root investment in response to moisture availability.

The PCA biplot (Figure 3.0.4) revealed clear genotype separation across water regimes. Tiga Nicuru DIP-C-F7471 and ARC under water-stressed conditions were positioned along the positive axis of PC1, aligning with traits indicative of deep, wide, and well-branched root systems. In contrast, DIP-C and TIGD showed displacement toward SMR and away from root architectural traits, suggesting limited adaptation to water stress. These results reinforce the importance of integrated root traits such as RSW, RDM, and TRL as functionally co-expressed indicators of drought resilience.

Overall, PCA highlights the central role of root architectural plasticity in mediating drought adaptation in Bambara groundnut. Genotypes with strong loadings for PC1 traits under stress conditions, particularly those maintaining coordinated development of root width, depth, and dry matter, represent promising candidates for selection in dryland breeding programmes.

3.3.3. Pearson correlation analysis of plant traits

Pearson correlation analysis (Figure 3.0.5) revealed several strong and biologically meaningful associations among root and shoot traits, reinforcing the interconnected nature of drought adaptation in Bambara groundnut. Convex hull area (CHA) was highly correlated with total root length (TRL; $r = 0.95$), root branch count (RBC; $r = 0.89$), root system width (RSW; $r = 0.97$), and root dry mass (RDM; $r = 0.88$), indicating that genotypes with broader lateral root spread also tend to develop deeper, more branched, and heavier root systems. TRL also showed strong positive correlations with root system depth (RSD; $r = 0.86$), total root volume (TRV; $r = 0.91$), and RDM ($r = 0.93$), highlighting the functional coordination between root elongation, volume, and biomass accumulation under water stress.

Above-ground traits were positively linked to root development. Shoot length (SL) correlated strongly with CHA ($r = 0.89$), TRL ($r = 0.90$), and SDM ($r = 0.84$), suggesting that a well-developed root system supports enhanced shoot growth. Root mass ratio (RMR) and root-shoot ratio (RSR) were negatively correlated with shoot mass ratio (SMR; $r = -0.77$ and –0.72, respectively), reflecting the expected trade-off in biomass allocation under drought, where stress-resilient genotypes invest more in root growth at the expense of shoots.

Table 3.0.4: Summary of factor loadings, eigenvalue measure of sampling adequacy, percent and cumulative variation for root traits

Variables	PC1	PC2	PC3
CHA	0.985	-0.095	-0.099
LA	0.819	0.505	0.023
RBC	0.920	0.054	-0.069
RDM	0.827	0.098	-0.031
RMR	-0.625	0.774	-0.072
RSD	0.982	0.096	0.002
RSR	-0.466	0.836	0.016
RSW	0.992	-0.013	0.023
SDM	0.855	0.473	0.198
SL	0.920	0.380	-0.005
SMR	0.625	-0.774	0.072
TLR	0.991	0.072	-0.105
Eigenvalue	8.680	2.555	0.078
Variability (%)	72.332	21.294	0.647
Cumulative %	72.332	93.626	100.000

convex hull area (CHA), shoot length (SL), total root length (TRL), root branch count (RBC), root system depth (RSD), leaf area (LA), root dry mass (RDM), shoot dry mass (SDM), whole plant dry mass (WPDM), root shoot ratio (RSR), shoot mass ratio (SMR), total root volume (TRV) and root mass ratio (RMR)

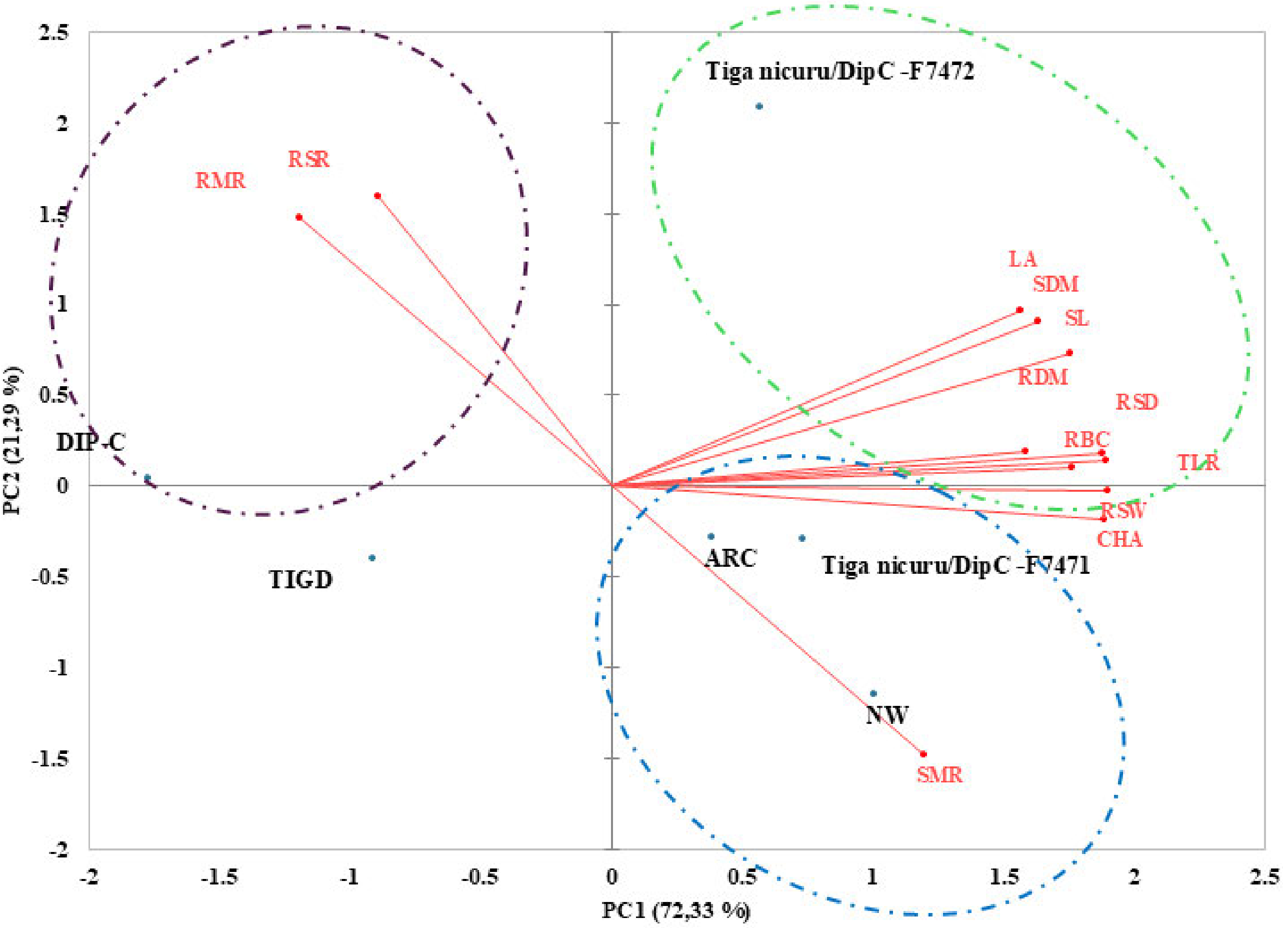
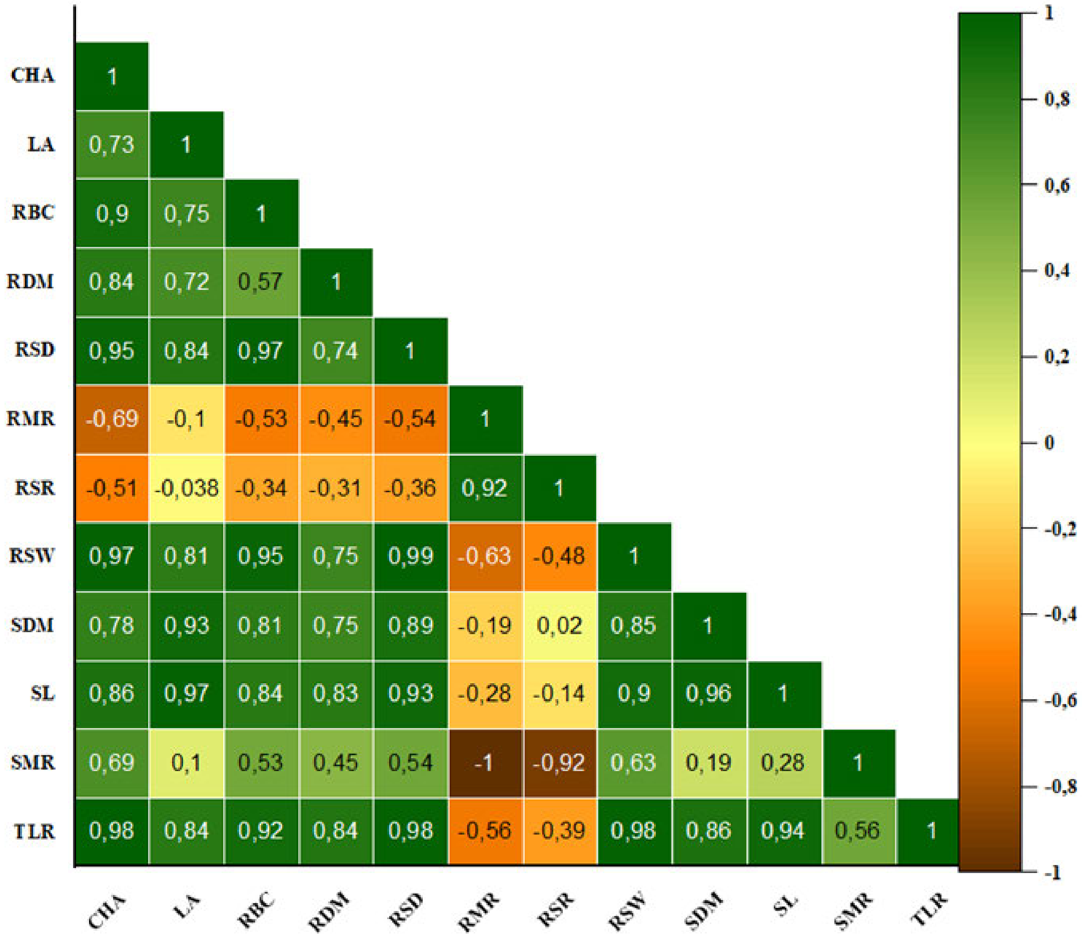


Figure 3.0.4: Principal component (PC) biplots demonstrating the relationships among root traits of six Bambara genotypes (ARC, N0v4, 519 and NW) at different water regimes no-stress (NS) and water-stressed (WS)



	CHA	LA	RBC	RDM	RSD	RMR	RSR	RSW	SDM	SL	SMR	TLR
CHA	1											
LA	0,73	1										
RBC	0,9	0,75	1									
RDM	0,84	0,72	0,57	1								
RSD	0,95	0,84	0,97	0,74	1							
RMR	-0,69	-0,1	-0,53	-0,45	-0,54	1						
RSR	-0,51	-0,038	-0,34	-0,31	-0,36	0,92	1					
RSW	0,97	0,81	0,95	0,75	0,99	-0,63	-0,48	1				
SDM	0,78	0,93	0,81	0,75	0,89	-0,19	0,02	0,85	1			
SL	0,86	0,97	0,84	0,83	0,93	-0,28	-0,14	0,9	0,96	1		
SMR	0,69	0,1	0,53	0,45	0,54	-1	-0,92	0,63	0,19	0,28	1	
TLR	0,98	0,84	0,92	0,84	0,98	-0,56	-0,39	0,98	0,86	0,94	0,56	1

Figure 3.0.5: Pearson correlation matrix showing pairwise relationships among root and shoot traits of Bambara groundnut genotypes across irrigation treatments**.**

Correlations were observed between convex hull area (CHA) and total root length (TRL), root branch count (RBC), root system width (RSW), and root dry mass (RDM, shoot length (SL), shoot dry mass (SDM) , shoot mass ratio (SMR), root mass ratio (RMR) and root-shoot ratio (RSR). Darker shades indicate stronger correlations; only significant correlations ($p < 0.05$) are shown.

3.4. Discussion

Drought remains a dominant constraint to crop productivity in sub-Saharan Africa, with yield reductions of up to 50% in staple crops linked to increasing aridity and erratic rainfall patterns (FAO, 2023, IPCC, 2023). This study provides important insights into the drought adaptation responses of Bambara groundnut, revealing significant genotypic variation in root and shoot traits under contrasting irrigation regimes. These differences have direct relevance for breeding efforts targeting resilience in dryland agriculture.

Analysis of variance (Table 3.0.3) revealed significant genotype × irrigation interactions for key root traits including convex hull area (CHA), root branch count (RBC), root system depth (RSD), root system width (RSW), root dry mass (RDM), and total root length (TRL). This highlights the presence of physiological plasticity, defined as the capacity of a genotype to adjust growth and allocation patterns in response to environmental stress (Gratani, 2014). As shown in Figure 3.0.3, ARC responded to water stress by increasing both rooting depth (12.2–19.9 cm) and root biomass (0.42–1.16 g), while maintaining a stable lateral spread. This reflects a coordinated drought-avoidance strategy that combines vertical root expansion with increased biomass allocation to enhance water uptake (Ghadirnezhad Shiade et al., 2023). In contrast, Tiga Nicuru DIP-C-F7471 also deepened its roots (11.0–14.5 cm) but exhibited a sharp decline in root system width (12.2–6.96 cm) and biomass (1.27–0.64 g), suggesting a more conservative strategy that prioritises accessing deeper moisture while limiting resource expenditure (Guo et al., 2024). Developing deeper roots allows plants to reach water unavailable to shallow systems, and narrowing the root system can improve water uptake efficiency at lower metabolic cost (Kalra et al., 2024). Similar trends have been reported by Lynch (2019), who found that crops with finer, deeper roots are better equipped to exploit subsoil moisture under drought conditions.

These contrasting patterns illustrate how genotypes express different drought-avoidance strategies, which may reflect a trade-off between acquisition efficiency and metabolic cost (Kooyers, 2015, Fang et al., 2017). ARC's deeper and denser root system aligns with high-input avoidance mechanisms, while DIP-C-F7471's reduced biomass may indicate a more conservative strategy optimised for stress environments (Lee and Suh, 2013, Liu et al., 2017).

Some legumes, such as common bean, faba bean, and soybean, tend to reduce root growth under drought conditions (Polania et al., 2017, Belachew et al., 2018, Gao et al., 2020), while chickpea shows genotype-specific responses depending on the type and timing of drought

(Ramamoorthy et al., 2017, Iseki et al., 2018). These interspecific differences further support the observed genotypic variation in Bambara groundnut and highlight the importance of screening for root traits when selecting for drought resilience.

In addition to root traits, Bambara groundnut genotypes differed significantly in shoot length (SL) and leaf area (LA) under water stress (Table 3.0.3), reflecting above-ground morphological diversity. This is consistent with previous reports on photoperiodic variation (Kendabie et al., 2020) and stress tolerance in this crop (Dhanaraj, 2018, Rahmah et al., 2020). Although biomass-related traits (RDM, SDM, RMR, SMR, RSR) did not show significant genotypic effects under optimal conditions, RSD and RSR consistently increased under stress (Table 3.0.3), indicating biomass reallocation toward roots a classic drought-avoidance mechanism (Kundy, 2019). Traits like CHA, RBC, and RDM remained relatively stable across treatments, suggesting they are environmentally robust and potentially useful as selection markers for drought tolerance.

Multivariate analysis confirmed these patterns. Principal Component 1 (PC1), which explained 72.3% of the total variation (Table 3.0.4; Figure 3.0.4), was driven by root traits (CHA, TRL, RSD, RSW, RBC) and SL. Genotypes such as ARC and DIP-C-F7471 grouped along PC1, indicating coordinated expression of root architectural traits under water-limited conditions. Similar results have been reported in chickpea (Santos et al., 2020) and bread wheat, where RSW was a major contributor to genotypic differences under drought (Arifuzzaman et al., 2020). The co-variation of RSW, TRL, and RDM observed in this study parallels findings in perennial grasses like *Lolium perenne*, where moisture availability controls horizontal and vertical root extension (Zhang et al., 2019).

The Pearson correlation matrix (Figure 3.0.5) further clarified these trait interactions. CHA correlated strongly with TRL ($r = 0.95$), RBC ($r = 0.89$), RSW ($r = 0.97$), and RDM ($r = 0.88$), reinforcing the association between lateral spread and increased root depth, branching, and biomass. Similar relationships have been documented in maize (Postma et al., 2014), and (Smith et al. (2014) also demonstrated that larger average root diameters lead to higher biomass accumulation. Positive associations between root traits and shoot performance (SL, SDM) observed here suggest that below-ground investment supports above-ground productivity under drought. SDM could serve as a useful proxy for root system performance, particularly in plant breeding programmes where large numbers of genotypes must be screened and direct root phenotyping is costly or impractical. Using SDM as an indirect indicator offers a rapid, inexpensive method to estimate root vigour and drought responsiveness. Negative correlations between shoot mass ratio (SMR) and both root mass ratio (RMR; r = –0.77) and root-shoot ratio (RSR; r = –0.72) indicate a clear trade-off in biomass allocation a useful sign of drought avoidance where plants shift resources from shoot growth toward root development to enhance water uptake under stress.These integrated findings validate the role of root traits in breeding for drought resilience in Bambara groundnut. Rhizotron systems enabled early-stage root phenotyping under controlled conditions, offering a replicable and non-destructive screening method.

Trait combinations involving TRL, RSW, RDM, and allocation metrics (RMR, RSR) emerged as promising indicators of drought-adaptive potential. These findings provide a strong foundation for breeding climate-smart Bambara groundnut varieties and can inform research into other underutilised legumes, such as pigeon pea and tepary bean, to support resilient agriculture in the face of climate variability.

3.5. Conclusion

This study highlights the critical role of root system traits in drought adaptation in Bambara groundnut, an underutilised legume with considerable promise for climate-resilient agriculture. The results reveal significant genotypic variation in traits such as root depth, lateral spread, branching pattern, and biomass allocation, with genotypes like Tiga Nicuru DIP-C-F7471 and ARC exhibiting superior performance under water stress. These landraces maintained coordinated development of traits linked to enhanced water uptake and survival, including deeper root systems and strategic biomass reallocation toward roots.

Multivariate (PCA) and correlation analyses further confirmed that traits such as total root length, root system width, convex hull area, and root dry mass are functionally interconnected. This trait complex may serve as a reliable marker set for identifying drought-resilient genotypes. Additionally, the observed negative associations between shoot and root biomass allocation reaffirm the adaptive trade-offs made by stress-tolerant plants, favouring below-ground investment during early growth under water-limited conditions.

Despite these valuable insights, several limitations should be acknowledged. The experiment was conducted under controlled greenhouse conditions using a rhizotron setup, which, while ideal for early-stage root visualisation does not fully replicate the complexity of field environments. Moreover, the study focused on the seedling stage (35 days post-emergence), capturing early root development rather than full-season growth. As root architecture continues to evolve throughout the plant's life cycle, it is essential that these findings be validated under field conditions and across multiple growth stages to assess their long-term relevance to drought adaptation and yield stability.

For future research, comparative studies with other drought-tolerant legumes such as pigeon pea and tepary bean are recommended. These crops differ in growth habits, phenology, and resource allocation strategies, and a cross-species evaluation under uniform stress conditions would provide deeper insight into the relative efficacy of their drought responses. Such work could identify not only superior genotypes within species but also guide crop choice and diversification strategies for different agroecological zones.

The successful application of rhizotron-based phenotyping in this study also highlights its broader potential for implementation across other legume species, particularly in early-stage screening for drought resilience. By integrating root trait assessment into legume improvement pipelines, especially for underutilised crops, researchers and breeders can more effectively identify and deploy resilient genotypes. This can contribute to the wider goal of achieving food and nutritional security in water-limited environments, while promoting agrobiodiversity and strengthening the resilience of smallholder farming systems.

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CHAPTER 4: STRUCTURAL AND PHYSIOLOGICAL SEED COAT ASSSESSMENT OF BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA (L.) VERDC.)* GENOTYPES

Abstract

Bambara groundnut (*Vigna subterranea*) is a drought-tolerant, nutrient-rich legume with significant potential to enhance food and nutritional security in sub-Saharan Africa (SSA). However, inconsistent seedling emergence limits its cultivation, particularly under rainfed, low-input conditions. This study investigated structural and physiological seed coat traits and their influence on hydration and germination performance across six genetically diverse Bambara groundnut genotypes. Seed coat colour was quantified using stereomicroscopy and tri-stimulus values (RGB). Seed coat thickness was measured using scanning electron microscopy. Hydration behaviour was assessed through imbibition tests over 36 hours, and germination was evaluated in a greenhouse measuring germination percentage (G), mean germination time (MT), uniformity (CVt), and mean germination rate (MR). Significant genotypic differences ($P< 0.01$) were observed across all traits. Seed coat thickness ranged from 72.23 µm in DIP-C to 125.57 µm in Tiga nicuru/DipC-F7445. Hue varied from 8.37° (dark purple) to 44.87° (light brown), while lightness ranged from 15.60% to 45.10%. Imbibition behaviour varied significantly among genotypes. Tiga nicuru/DipC-F7445 exhibited the highest water uptake of 17–18% after 36 hours, with the fastest imbibition rate of 2.748 % h^{-1}, while DIP-C showed the lowest hydration of 9.0%, at a rate of 1.488 % h^{-1}. Germination percentages remained high across genotypes, ranging from 86.22% in Tiga nicuru/DipC-F7471 to 97.67% in DIP-C. Mean germination time varied from 14 days in Tiga nicuru/DipC-F7445 to 23 days in DIP-C. Tiga nicuru/DipC-F7445, characterised by a thick, dark seed coat, combined rapid imbibition with the fastest and most uniform germination performance (CVt = 32.95%).These findings reveal genetic diversity offering opportunities for breeding genotypes that tie rapid, uniform germination with favourable seed traits to improve crop establishment under climate variability. Future work should investigate tannin content and biochemical traits linked hydration dynamics and nutritional quality, crucial for realising Bambara groundnut's role in climate-resilient food and nutrition security.

Keywords: Germination, legumes, imbibition, seedling vigour, landrace variability

4.1. Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc.) is a drought-tolerant, nutrient-dense legume with considerable potential to enhance food and nutritional security in SSA (Nwadi et al., 2020, Mubaiwa et al., 2018). In Southern Africa, where smallholder farmers face increasing challenges from erratic rainfall, prolonged dry spells, and declining soil fertility (Lottering et al., 2021), this underutilized crop offers a promising alternative to conventional staples that underperform under stress (Olanrewaju et al., 2022, Gerrano et al., 2021). Average yield losses in rainfed systems across the region can reach up to 40% due to drought and delayed rainfall onset (FAO, 2017). The sampling relies on climatic conditions such as the rain that is expected on those date and if missed it will be difficult to find another rainy period during this winter. Second, we were only granted access to the farms only for those dates. Further, the student has been in the system for long time and the research was delayed due to past financial constraints

Bambara groundnut suitability to low-input systems, adaptability to marginal environments, and soil-enriching properties position it as a strategic resource for building climate-resilient food systems. Despite its agronomic and nutritional value, Bambara groundnut remains neglected in formal seed systems, breeding programs, and policy frameworks (Khan et al., 2021, Oyeyinka et al., 2021). Globally, it is grown on about 0.37 million hectares, yielding around 0.22 million tons of shelled grain annually (FAOSTAT, 2020). West Africa, its genetic diversity center, contributes roughly 65% of global output (Majola et al., 2021).

Yet, most African countries cannot meet domestic demand, with production largely consumed or traded locally, limiting global market penetration (Mayes et al., 2019). A key constraint to wider cultivation is inconsistent seedling establishment (Kunene et al., 2024), undermining yield stability. Poor germination is common in smallholder systems where seeds are sown into dry or variably moist soils. Such conditions cause delayed or staggered emergence, resulting in sparse stands, higher weed pressure, and inefficient resource use (Muhammad et al., 2016). Field observations show uneven emergence can cut yields by up to 35%, especially in moisture-limited, low-input settings (Waqas et al., 2019).

This issue is particularly urgent given that over 95% of agriculture in SSA is rainfed, and smallholders contribute more than 80% of the region's food supply (AUDA-NEPAD, 2022). Ensuring rapid and uniform crop establishment is critical to safeguarding productivity and resilience in smallholder systems.

A key but underexplored factor contributing to establishment variability lies in the physical and physiological properties of the seed. Beyond offering structural protection, the seed coat regulates water absorption, gas exchange, solute retention and protection against imbibitional injury during germination (Upretee et al., 2024). In legume crops, coat thickness, permeability, and colour have been shown to influence hydration behavior and early seedling performance (Quilichini et al., 2022). In Bambara, where landraces display considerable variation in seed coat morphology, these traits may underlie observed differences in germination speed, uniformity and seedling vigour across environments (Baloyi and Swanepoel, 2023). Some landraces take up to 21 days to fully emerge, with hard-seededness and slow water uptake frequently reported as limiting factors (Mall, 2017, Berchie et al., 2010).

Although previous studies (Mandizvo and Odindo, 2019, Chibarabada et al., 2014) and more recent work such as Baloyi and Swanepoel (2023) have examined seed coat colour and its association with morphological or agronomic traits. Few studies have investigated the physiological and structural properties of seed coats such as permeability, hydration rate, solute leakage and their role in influencing germination dynamics and early seedling vigour. These functional traits remain poorly characterized in Bambara groundnut, limiting the development of targeted strategies to improve crop establishment. Understanding how seed coat characteristics affect water uptake and seedling performance is critical for informing breeding and seed system interventions, particularly in moisture-limited environments.

This study investigated the seed coat characteristics of genetically diverse Bambara groundnut recombinant inbred lines (RILs) and assessed their influence on water imbibition, solute leakage, germination dynamics, and seedling vigour. The research aimed to support seed selection and breeding strategies aligned with the needs of low-input, rainfed farming systems in Southern Africa by identifying trait combinations associated with improved establishment, particularly under moisture-limited conditions. Ultimately, the study contributed to efforts to enhance the performance, reliability, and resilience of Bambara groundnut in the face of increasing climatic uncertainty.

4.2. Materials and methods

4.2.1 Plant Material

Six Bambara groundnut genotypes were obtained from the University of KwaZulu-Natal's Bambara groundnut germplasm collection (Table 4.0.1). Seeds were harvested during the same growing season and stored under controlled ambient conditions until use to ensure uniformity and minimize variation due to environmental history.

Table 4.0.1: List of selected Bambara groundnut genotypes

Genotype	Colour	Origin
ARC	Brown	South Africa
Tiga nicuru/DipC -F7471	Red	Mali
Tiga nicuru/DipC -F7445	Purple	Mali
NW	White	Namibia
Tiga nicuru/DipC -F7472	Light brown	Mali
DIP-C	White/Cream	Botswana

4.2.2 Seed colour

Seed coat colour was assessed (Figure 4.0.1) on harvested seed samples using a stereomicroscope connected to computer software (Leica Application Suite 4.0, South Africa). The red, green and blue (RGB) colour values were recorded and then converted into hue (H), saturation (S) and lightness (L), following the method described by Bautista et al. (2014).

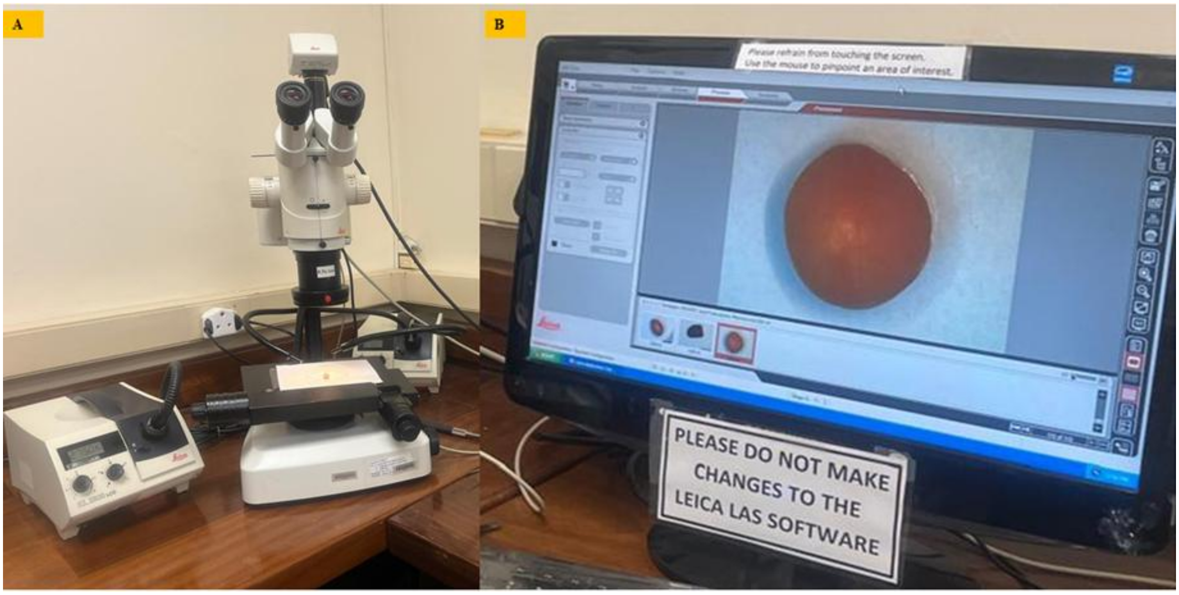

Figure 4.0.1: Equipment and software used for seed coat colour analysis. (A) stereomicroscope was used for imaging seed samples; (B) Bambara groundnut seed was visualised and analysed on a computer

4.2.3 Seed coat trait characterisation

Seed coat thickness was determined with a Zeiss EVO scanning electron microscope (SEM) (Zeiss, Oberkochen, Germany) (Figure 4.0.2). Seeds were cryofractured in liquid nitrogen and then split in half. They were mounted on stubs and fixed in place using carbon insulating tape. A gold coating was applied to the samples using a Quorum Q150R ES sputter coater before examination under the Zeiss EVO SEM operating in high vacuum mode. Images were taken at an accelerating voltage of 5 kV, and both the seed coat thickness and its attachment to the cotyledon were measured using analysis software (Soft Imaging System, Münster, Germany)..

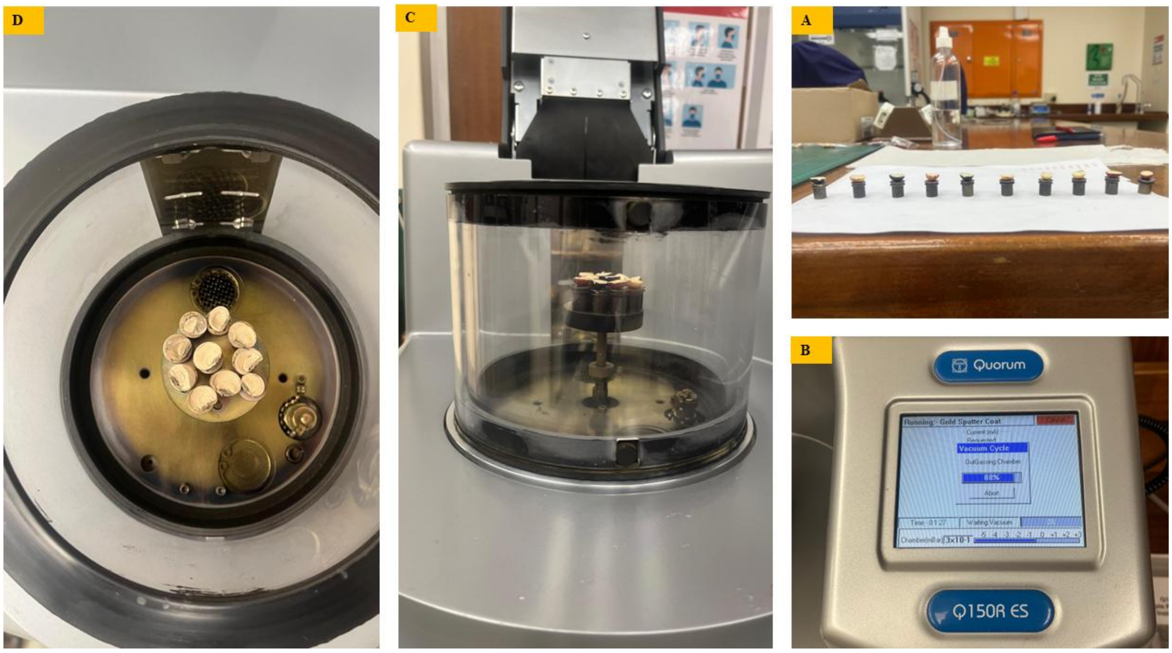

Figure 4.0.2: Preparing seed coat samples for scanning electron microscopy imaging. (A) seeds cryofractured in liquid nitrogen, split in half, and mounted on stubs using carbon adhesive tape; (B) gold coating of samples using a Quorum Q150R ES sputter coater; (C) samp samples placed inside the sputter coater chamber during the coating process; (D) close-up view of gold-coated seeds mounted on stubs, ready for SEM imaging.

4.2.3 Imbibition analysis

Imbibition curves (Equation 1) were determined by soaking seeds and recording the percentage increase in weight over time. Measurements were taken at four intervals: 0 h, 12 h, 24 h, and 36 h after sowing. For each genotype, the percentage of water uptake at each time point was calculated as described by Bewley et al. (2013):

$$Imbibition\ (\%) = \frac{W_t - W_0}{W_0} \times 100 \qquad (1)$$

where:

- W_t = weight of the seeds at time *t*
- W_0= initial dry weight of the seeds.

Linear regression analysis was performed for each genotype to model the increase in imbibition percentage over time. The intercept obtained from each regression equation represented the estimated initial imbibition percentage at time zero.

4.2.4 Germination tests and calculations

Germination setup

Germination experiments were conducted using 15 seeds per replicate, with three replicates assigned to each genotype. Seeds were sown directly into 10L thermoform pots filled with 30 dm^3 of Gromor Potting Mix, a sterile commercial medium chosen to ensure uniform texture, drainage, and nutrient conditions across all treatments. Before sowing, each pot was moistened with 250 mL of water to standardise initial soil moisture. Germination was monitored over 24 days, with seeds considered germinated once the radicle protruded at least 2 mm. The trials took place in a greenhouse at the Controlled Research Facility (CERU), University of KwaZulu-Natal, Pietermaritzburg, South Africa (29°37′37.5″ S; 30°24′10.4″ E), where environmental conditions were maintained at an average temperature of 25 ± 2 °C and relative humidity of 60 ± 3%. Pots were arranged randomly on raised benches and irrigated with 250 ml of tap water every two days, with watering schedules adjusted as needed to avoid either water stress or excess moisture. Germination counts were recorded at each observation interval, and germination parameters were computed following the methods described by Ranal et al. (2009):

Germinability (G)

Germination percentage (G) (Equation 2) represents the percentage of seeds that successfully germinate and was calculated as described by Ranal et al. (2009):

$$G = \frac{\Sigma n_i}{N} \; x \; 100 \qquad (2)$$

where:

- n_i = number of seeds germinated at time t_i
- N = total number of seeds tested.

Mean Germination Time (MT)

Mean germination time (MT) (Equation 3) reflects the average time taken for seeds to germinate and was calculated as described by Ranal et al. (2009):

$$MT = \frac{\Sigma(n_{i\,x\,t_i})}{\Sigma n_i} \qquad (3)$$

where:

- t_i = time from sowing to observation *i* (days or hours).

Coefficient of Variation of Germination Time (CVt)

The uniformity of germination (Equation 4) was assessed through the coefficient of variation of germination time (CV_t), calculated as described by Ranal et al. (2009):

$$CV_t = \frac{S_t}{MT} x\, 100 \qquad (4)$$

where S_t is the standard deviation (Equation 5) of germination times described by Ranal et al. (2009):

$$S_t = \sqrt{\frac{\sum n_i(t_i - MT)^2}{\sum n_i - 1}} \qquad (5)$$

Mean Germination Rate (MR)

Mean germination rate (MR) (Equation 6) was calculated as the reciprocal of mean germination time as described by Ranal et al. (2009):

$$MR = \frac{1}{MT} \qquad (6)$$

4.2.5 Statistical Analysis

All statistical analyses were performed using Genstat software (VSN International, Release 23.1). Data was subjected to analysis of variance (ANOVA) to determine the effect of genotype on germination parameters. Significant differences among means were identified using Fisher's protected least significant difference (LSD) test at the 5% probability level.

4.3. Results

4.3.1 Seed coat morphology

Analysis of variance revealed significant genotypic differences ($p < 0.01$) for all measured seed coat traits, including hue, saturation, lightness, and thickness (Table 4.0.2). Hue, lightness, and saturation values were used to quantitatively describe seed coat colour, providing an objective basis for comparing colour type, pigmentation intensity, and brightness among genotypes.

Hue values varied from 8.37° in Tiga nicuru/DipC -F7445 (purple) to 44.87° in Tiga nicuru/DipC -F7472 (light brown), demonstrating differences from deeply pigmented to lighter-coloured seed coats. Lightness values followed a similar trend, with darker seeds such as Tiga nicuru/DipC -F7445 (16.93%) and Tiga nicuru/DipC -F7471 (15.60%) showing the lowest brightness, while NW (45.10%) and DIP-C (43.17%) exhibited the highest lightness levels. Saturation also differed significantly across genotypes, ranging from 55.43% in NW to 92.07% in Tiga nicuru/DipC -F7445, highlighting substantial variation in colour intensity (Table 4.0.3).

Significant variation was also observed in seed coat thickness among the six genotypes ($p < 0.01$) (Figure 4.0. 3). Tiga nicuru/DipC -F7445 exhibited the thickest seed coat (approximately 125 µm), followed by Tiga nicuru/DipC -F7471. In contrast, DIP-C and NW recorded the thinnest coats, both below 80 µm. ARC and Tiga nicuru/DipC -F7472 showed intermediate thickness values. Differences among genotypes were statistically significant, as indicated by the LSD of 15.36 µm and a coefficient of variation of 9.5% (Figure 4.0.4).

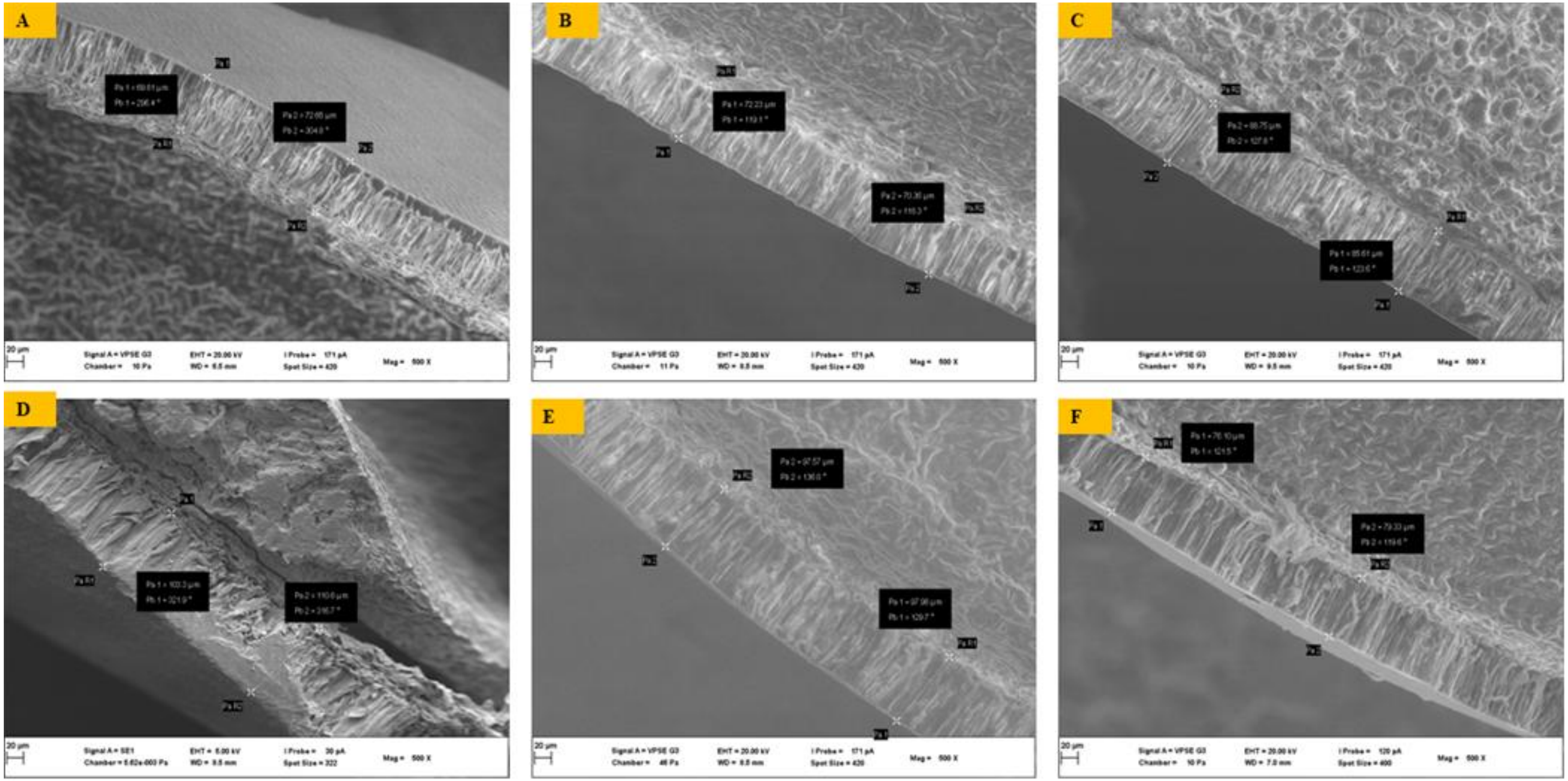

Figure 4.0.3: Seed coat thickness of six Bambara groundnut measured using scanning electron microscope

Table 4.0.2: Analysis of variance (ANOVA) for hue, saturation, lightness and seed coat thickness among six Bambara groundnut genotypes

Source of variation	d.f	Hue	Lightness	Saturation	Seed coat thickness	Water imbibition
Genotype (G)	5	988.83**	521.78**	742.78**	1352.74**	72.1482**
Residual	12	23.68^{NS}	15.33^{NS}	86.45^{NS}	74.56^{NS}	0.8615^{NS}

d.f; degrees of freedom, NS= not significant. *= $P < 0.05$; **= $P < 0.01$.

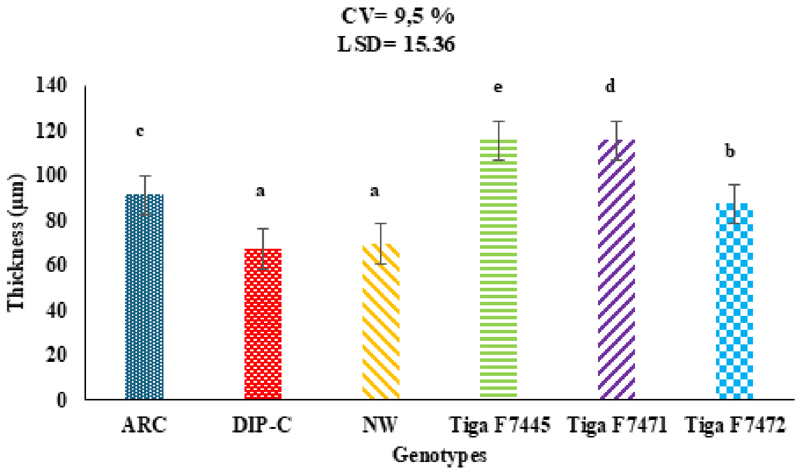

Figure 4.0.4: Mean seed coat thickness (µm) of six Bambara groundnut genotypes

Bars represent means ± SE (n = 3). Different letters above bars indicate significant differences at $p < 0.05$ (LSD = 3.412; CV = 2.2%)

Table 4.0.3: Mean values of seed coat colour traits (hue, saturation, lightness) across six Bambara groundnut genotypes

Genotype	Hue (°)	Saturation (%)	Lightness (%)
ARC	13.20 ^{a}	77.80 ^{bc}	20.57 ^{a}
DIP-C	42.63 ^{b}	59.13 ^{a}	43.17 ^{c}
NW	44.33 ^{b}	55.43 ^{a}	45.10 ^{c}
Tiga nicuru/DipC -F7445	8.37 ^{a}	92.07 ^{c}	16.93 ^{a}
Tiga nicuru/DipC -F7471	11.27 ^{a}	90.03 ^{c}	15.60 ^{a}
Tiga nicuru/DipC -F7472	44.87 ^{b}	65.20 ^{ab}	32.67 ^{b}
CV (%)	17.7	12.7	13.5

Different letters within columns indicate significant differences at $p < 0.05$ based on the Least Significant Difference (LSD) test. CV = coefficient of variation.

4.3.2 Hydration behaviour

Significant genotypic differences ($p < 0.01$) (Table 4.0.2) were observed in the hydration behaviour of Bambara groundnut seeds during imbibition, measured over 36 hours (Figure 4.0.5 and Table 4.0.4). All genotypes exhibited a progressive increase in imbibition percentage, but with distinct differences in initial water uptake, the rate of increase, and final hydration levels. Tiga nicuru/DipC-F7445 showed the highest hydration performance, starting at approximately 6.4% imbibition and rising steadily to reach around 17–18% at 36 hours. This genotype also exhibited the highest rate of imbibition (2.748 % h^{-1}), indicating rapid water absorption across the entire period. DIP-C consistently maintained the lowest hydration levels, with an initial imbibition of about 3.9% and only modestly increasing to roughly 9% by 36 hours. Its rate of imbibition was moderate (1.488 % h^{-1}) relative to other genotypes, confirming its slower water uptake.ARC began at 8.6% and reached around 13–14% at the end of the experiment, with a rate of imbibition of 1.224 % h^{-1}. NW initially measured approximately 3.0%, increasing to about 12–13% at 36 hours, supported by a rate of imbibition of 1.712 % h^{-1}.Tiga nicuru/DipC-F7471 started at 8.7% and followed a similar trajectory to ARC, ending at around 13–14%, but with a slightly lower rate of imbibition (1.165 % h^{-1}). Tiga nicuru/DipC-F7472 had the highest initial imbibition (9.8%) among all genotypes, but its water uptake progressed more slowly during the early hours, followed by a sharper increase after 24 hours, ultimately reaching approximately 15–16% at 36 hours. It recorded the lowest rate of imbibition overall (0.751 % h^{-1}), indicating a delayed but eventual increase in water uptake.

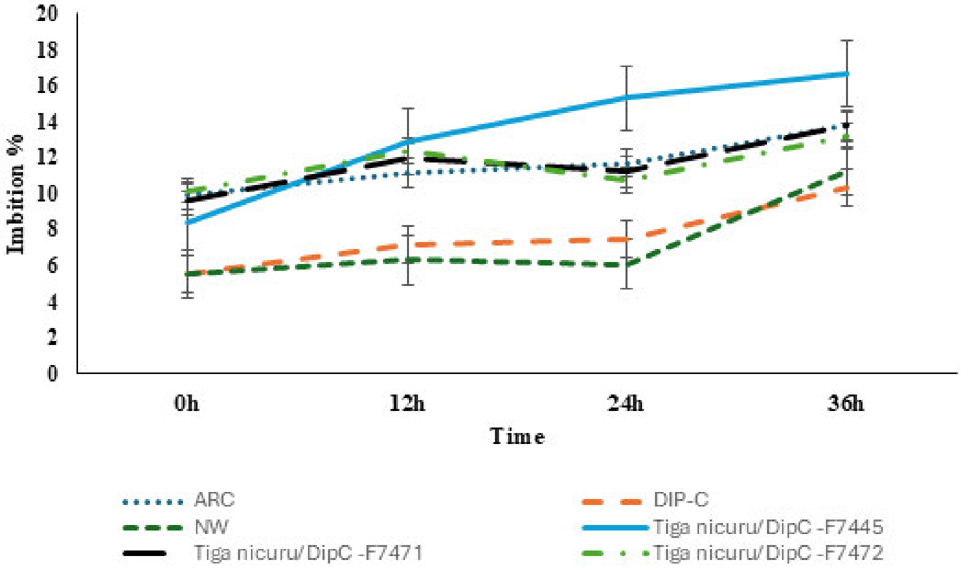

Figure 4.0.5: Changes in imbibition percentage over time (0 h, 12 h, 24 h, and 36 h) for six Bambara groundnut genotypes: ARC, NW, DIP-C, Tiga nicuru/DipC-F7445, Tiganicuru/DipC-F7471, and Tiga nicuru/DipC-F7472. Values represent means ± standard error

Table 4.0.4 : Rates of seed imbibition (% h^{-1}) among six Bambara groundnut genotypes

Genotype	rate of imbibition (% h^{-1})
ARC	1.224
DIP-C	1.488
NW	1.712
Tiga nicuru/DipC -F7445	2.748
Tiga nicuru/DipC -F7471	1.165
Tiga nicuru/DipC -F7472	0.751

4.3.3 Germination performance

Analysis of variance (Table 4.0.5) revealed highly significant differences (P< 0.01) among the six Bambara groundnut genotypes for all germination parameters measured, including germination percentage(G), mean germination time (MT), coefficient of variation of germination time (CVt), and mean germination rate (MR). As shown in Table 4.0.6, G was generally high across genotypes, ranging from 86.22% in Tiga nicuru/DipC-F7471 to 953% in ARC, with ARC and DIP-C exhibiting the highest values. Mean germination time varied considerably, with Tiga nicuru/DipC-F7445 demonstrating the fastest germination at 14 days, while DIP-C required the longest time to germinate at 23 days.

The uniformity of germination, indicated by CVt, was highest in DIP-C (58.33%), suggesting greater variability among seeds, whereas Tiga nicuru/DipC-F7445 displayed the lowest CVt (32.95%), indicating more consistent germination. Mean germination rate also differed significantly among genotypes, with Tiga nicuru/DipC-F7445 achieving the highest rate (0.00373 day-1), while DIP-C recorded the lowest (0.00040 day-1). Table 4.6 highlights substantial genotypic variation in the speed and uniformity of germination among the evaluated Bambara groundnut genotypes

Table 4.0.5: Analysis of variance (ANOVA) for germination parameters among six Bambara groundnut genotypes.

Source of variation	d.f	CV_t	G	MR	MT
Genotype (G)	5	486.93 **	43.56 **	0.1201 **	31.829 **
Residual	12	17.87 ^{NS}	12.43 ^{NS}	0.00055 ^{NS}	2.273 ^{NS}

d.f; degrees of freedom, NS= not significant. *= P < 0.05; **= P < 0.01. Shown are F-values and their significance levels for each trait: G = germinability; MT = mean germination time; CVt = coefficient of variation of germination

Table 4.0.6: Germination parameters (mean ± standard error) for six Bambara groundnut genotypes.

Genotype	G (%)	MT (days)	CVt (%)	MR (day^{-1})
Tiga nicuru/DipC-F7445	92.00 ± 2.88 ^{ab}	13.85 ± 1.23 ^{a}	32.95 ± 3.45 ^{a}	0.00373 ± 0.01922 ^{a}
Tiga nicuru/DipC-F7472	93.11 ± 2.88 ^{b}	15.11 ± 1.23 ^{ab}	39.38 ± 3.45 a	0.00219 ± 0.01922 ^{a}
Tiga nicuru/DipC-F7471	86.22 ± 2.88 ^{a}	18.86 ± 1.23 c	47.34 ± 3.45 ^{b}	0.00106 ± 0.01922 ^{a}
ARC	95.00 ± 2.88 ^{b}	17.79 ± 1.23 ^{bc}	49.18 ± 3.45 b	0.49185 ± 0.01922 b
NW	93.11 ± 2.88 ^{b}	19.62 ± 1.23 ^{c}	68.28 ± 3.45 d	0.00085 ± 0.01922 ^{a}
DIP-C	97.67 ± 2.88 ^{b}	22.91 ± 1.23 ^{d}	58.33 ± 3.45 ^{c}	0.00040 ± 0.01922 ^{a}
LSD	**6.271**	**2.682**	**7.521**	**0.04188**

G = germinability; MT = mean germination time; CVt = coefficient of variation of germination time; MR = mean germination rate. Letters indicate groups of means that do not differ significantly according to Fisher's protected least significant difference test at the 5% probability level.

4.4. Discussion

The results of this study highlight significant genotypic variation in seed coat traits, water absorption patterns, and germination behaviour among six Bambara groundnut genotypes. This discussion explores how seed coat morphology and physiology may contribute to differences in seedling establishment and what these findings mean for breeding and cultivation under rainfed, low-input conditions in sub-Saharan Africa (SSA).

Variation in seed coat colour traits, including hue, saturation, and lightness, was pronounced across genotypes (Tables 4.0.2 and 4.0.3; Figures 4.0.3 and 4.0.4). Dark-coloured genotypes, such as Tiga nicuru/DipC-F7445 and Tiga nicuru/DipC-F7471, showed low hue and lightness values and high saturation, while NW and DIP-C exhibited lighter colours and lower saturation. These differences are consistent with previous reports suggesting that pigmentation is genetically controlled and may reflect ecological adaptations, such as protection against ultraviolet radiation, pathogens, or mechanical damage (Radchuk and Borisjuk, 2014, Stetter et al., 2020).

Studies in other legumes, like common bean, have shown that variation in seed coat colour is linked to physiological traits such as tannin content and permeability, influencing seed quality and germination performance (Caldas and Blair, 2009). In common bean, darker seed coats correlate with higher condensed tannin levels, offering protective benefits but potentially affecting water uptake and nutrient bioavailability (Constabel et al., 2014). Although tannin content was not directly measured here, the marked pigmentation differences in Bambara groundnut suggest possible biochemical variations that could influence permeability and hydration. Understanding these relationships is crucial for selecting genotypes with desirable seed coat traits and optimal germination, especially under moisture-limited conditions in SSA.

Seed coat thickness also varied significantly ($p < 0.01$) among genotypes. Tiga nicuru/DipC-F7445 exhibited the thickest seed coat, exceeding 120 µm, whereas DIP-C and NW had much thinner coats below 80 µm (Figure 4). Thicker seed coats are often physical barriers that slow water absorption, contributing to dormancy (Wu and Shen, 2021; Abati et al., 2022). However, our findings suggest that thickness alone does not determine permeability. For example, Tiga nicuru/DipC-F7445 had both a thick seed coat and rapid water uptake, highlighting that internal seed coat structure and biochemical composition are also crucial. Mandizvo and Odindo (2019) noted that legume seed coats contain waxes, cellulose complexes, and phenolic compounds like tannins, which can strengthen the coat and impact water movement. Differences in microstructure, micropores, or chemical composition could explain why thick-coated seeds in this study showed high water uptake, aligning with observations by Chibarabada et al. (2014).

Hydration behaviour further differentiated the Bambara groundnut genotypes, with significant genotypic effects ($p < 0.01$) observed in both initial water uptake and subsequent imbibition rates (Table 4.0.4; Figure 4.0.5). Among the genotypes, Tiga nicuru/DipC-F7445 exhibited high initial water absorption, starting at approximately 6.4% imbibition, and achieved the highest final imbibition percentage of 17–18% after 36 hours. It also recorded the highest rate of imbibition at 2.748 % h^{-1}, indicating rapid water absorption throughout the period. This pattern aligns with observations by Mandizvo (2019), who noted that dark-coloured seeds can imbibe water more rapidly, likely due to microstructural features such as the hilum, micropyle, or raphe facilitating water entry (Luan et al., 2017, Wu and Shen, 2021).

Similar trends have been documented in crops like chicory, peas, and cowpeas, where darker seeds sometimes display faster water uptake than lighter seeds, attributed to specific anatomical adaptations (Bertling et al., 2016, Bhatla and Lal, 2023). These findings indicate that seed coat thickness alone does not govern imbibition rates, but rather, internal structural pathways and seed coat composition also play crucial roles.

DIP-C, characterised by a lighter seed coat, showed both the lowest initial water uptake of 3.9% and the lowest cumulative hydration, reaching only about 9.0% after 36 hours. It also exhibited a comparatively lower rate of imbibition of 1.488 % h^{-1}. This outcome partly contradicts the findings of Chibarabada et al. (2014), who reported faster water absorption in lighter-coloured Bambara groundnut seeds. The reduced imbibition in DIP-C may be attributable to factors such as denser seed coat tissue, the presence of uniform waxy layers, or chemical barriers like lignin and suberin, all of which can reduce water permeability (Bewley et al., 2013).

These differences in hydration significantly affected germination. High germination percentage (>90%) was observed across genotypes, but they differed markedly in speed and uniformity (Tables 4.0.5 and 4.0.6). Parameters like mean germination time (MT), germination uniformity (CVt), and mean germination rate (MR) provide crucial insights for rainfed systems where rapid establishment is essential (Khajeh-Hosseini et al., 2009, Finch-Savage and Bassel, 2016).

Tiga nicuru/DipC-F7445 showed a favourable combination of high germination (92%), fast germination (MT of 14 days), and synchronised emergence (CVt of 32.95%). This rapid, uniform emergence is advantageous for rainfed farming, where seedlings must establish quickly before soil moisture declines. DIP-C, despite high germination (97.67%), required 23 days to complete germination and showed higher variability (CVt of 58.33%). Such delays and uneven germination are risky in smallholder systems exposed to erratic rainfall, as seeds may lose viability or fail to synchronise with moisture availability (Long et al., 2015). Although delayed germination may serve as a bet-hedging strategy to avoid false starts in rainfall (Pausas et al., 2022, Gremer and Venable, 2014), it is less desirable in resource-constrained contexts where reliable establishment is critical.

This study reveals that seed coat traits, hydration behaviour, and germination outcomes are interrelated but complex. While lighter seeds are often assumed to imbibe water faster, our results show that dark, thick-coated genotypes like Tiga nicuru/DipC-F7445 can also achieve rapid hydration and germination. This underscores the importance of genotype-specific anatomical and physiological factors beyond simple physical barriers (Upretee et al., 2024)

Important to mention, the genotypes in this study are recombinant inbred lines developed through breeding efforts, which may have introduced unique structural or biochemical adaptations, altering typical seed coat–germination relationships. This explains why our findings sometimes differ from earlier reports and highlights the value of breeding for improved seed coat traits to enhance Bambara groundnut resilience under changing climatic conditions.

4.5. Conclusion

This study demonstrated significant genotypic variation in seed coat morphology, hydration behaviour, and germination performance among Bambara groundnut genotypes, highlighting their critical roles in seedling establishment. Contrary to the expectation that thick, dark seed coats hinder water uptake, Tiga nicuru/DipC-F7445 combined a thick, deeply pigmented coat with rapid imbibition and the fastest, most uniform germination. In contrast, despite high germinability, genotypes like DIP-C showed slower and less uniform germination, underscoring that seed viability alone does not guarantee successful establishment.

These findings confirm that seed coat traits in Bambara groundnut influence water uptake dynamics and germination speed, which are crucial for crop establishment, especially in rainfed systems facing erratic rainfall and drought stress in sub-Saharan Africa. The observed variability in seed traits and germination performance reflects significant genetic diversity within Bambara groundnut, presenting valuable opportunities for breeding programmes. Harnessing this diversity to combine rapid and uniform germination with favourable seed coat properties will improve crop establishment and resilience under climate variability and water stress.

However, this study did not investigate the tannin content and other polyphenolic compounds within the seed coats, which are known to affect both seed coat permeability and nutritional quality. Future research should examine how the structural and physiological traits identified here relate to biochemical components such as tannins, as these compounds can influence not only germination behaviour but also nutritional value, mineral bioavailability, and potential health benefits. Integrating physiological insights with nutritional profiling will be essential to fully harness Bambara groundnut's potential as a climate-resilient crop that supports both food security and improved nutrition, particularly in the context of a growing population and the challenges posed by climate change.

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CHAPTER 5: EFFECT OF HYDROPRIMING ON SEEDLING GROWTH OF DIFFERENT BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA (L.) VERDC.)* LANDRACES

Abstract

Bambara groundnut (*Vigna subterranea (L.) Verdc.)* is a drought-tolerant, underutilised legume with the potential to improve food security, but its slow, uneven germination due to hard seed coats constrains cultivation. This study investigated the effects of hydropriming (0, 12, 24, and 36 h) on the seed imbibition, emergence, and early seedling growth in four landraces (NW, Nov4, ARC, and 519) under greenhouse conditions. The results showed genotype-specific variation in the water uptake, with Genotype 519 exhibiting the highest water imbibition (17.31%) at 36 h, while NW dis-played slower but steadier hydration (13.51%). These differences reflect contrasting seed coat permeability and hydration strategies, which influenced the subsequent emergence patterns. Hydropriming significantly reduced the time to emergence (50% emergence by Day 5 in NW) and increased the seedling vigour. On average across all genotypes, after 9 days of growth, the shoot length increased from 7.8 cm to 12.7 cm, the root length from 11.6 cm to 18.1 cm, and the dry mass from 0.38 g to 0.67 g. Analysis of variance (ANOVA) revealed significant effects ($p < 0.01$) interaction of the genotype, the priming duration, on traits such as the root length, dry mass, and root-to-shoot ratio. PCA identified the whole-plant dry mass, root dry mass, and root-to-shoot ratio as key contributors to performance. Pearson correlation showed a strong positive association ($r = 1.0$, $p < 0.001$) between the priming duration and seedling biomass, although the extended imbibition time may partially explain this trend. Hydropriming, particularly for 36 h, showed promise in promoting early growth, indicating that it is a favourable low-cost intervention. Field-level validation is recommended to assess the practical scalability under diverse environmental conditions.

Keywords: underutilised crop; germination; legume; drought resilience; climate-smart agriculture

5.1. Introduction

Bambara groundnut (*Vigna subterranea (L.) Verdc.)* is a hardy, drought-tolerant legume indigenous to sub-Saharan Africa, where it is cultivated primarily by small-holder farmers (Mayes et al., 2019). It is rich in carbohydrates (63–69%) and protein (18–24%), and it contains essential amino acids such as lysine and methionine, making it a valuable contributor to food and nutritional security in resource-poor environments (Mubaiwa et al., 2018, Tan et al., 2020).

According to FAO estimates, the global annual production of Bambara groundnut is estimated to be 0.2 million tonnes from an area of 0.25 million hectares worldwide (FAOSTAT, 2020). West Africa is the main Bambara groundnut production region in SSA, where Burkina Faso, Niger, and Cameroon are the leading producers, contributing to 74% of the global production (Majola et al., 2021, Soumare et al., 2022). Despite its agronomic potential and resilience to marginal growing conditions, Bambara groundnut (BGN) remains underutilised in formal agricultural systems due to low yields (~0.8 t/ha), poor market integration, and inconsistent germination (Olanrewaju et al., 2022, Zulu and Modi, 2010).

As efforts to mainstream climate-resilient agriculture intensify, BGN has received renewed attention for its adaptability to low-input farming systems and its potential to diversify cropping portfolios in drought-prone regions (Khan et al., 2021, Waqas et al., 2019). However, one of the key physiological constraints limiting its wider adoption is the hard seed coat (Marthandan et al., 2020, Obura et al., 2021), which impedes water uptake, delays germination (up to 21 days), and leads to variable seedling establishment (Sen et al., 2021). These delays are particularly detrimental in environments with short rainfall windows, where rapid and uniform emergence is critical for crop success and yield stability.

Seed priming, a pre-sowing treatment involving controlled hydration followed by re-drying, has emerged as a practical technique to overcome dormancy and enhance seed performance (Samota et al., 2017, Jarrar et al., 2023). It initiates key metabolic processes that improve water up-take, enzymatic activity, and protein synthesis, resulting in faster and more uniform seedling emergence (Tabassum et al., 2018, Afzal et al., 2020). Among the various priming methods, hydropriming, a method that involves soaking seeds in water for a defined period, is the most accessible and environmentally sustainable (Sen et al., 2021). It requires no specialised inputs, making it especially suitable for smallholder farmers who often face economic and infrastructural constraints (Zaman et al., 2017).

Previous research has demonstrated the effectiveness of hydropriming in im-proving seedling vigour and early growth across major crops such as rice, wheat, sunflower, pigeon pea, and chickpea (Sajjan et al., 2017, Kumeera et al., 2018, Perera et al., 2023, Bewley et al., 2013). However, its efficacy is highly genotype-dependent, with the optimal soaking durations varying widely across species and cultivars. Excessive priming can also lead to reduced viability due to over-imbibition or premature radicle protrusion (Bewley et al., 2013). In the case of BGN, although there is growing interest in seed enhancement technologies such as biopriming, nutripriming, and treatments using compost tea or livestock urine (Bewley et al., 2013), many of these methods are either re-source-intensive or lack scalability in smallholder contexts.

Furthermore, while some studies on BGN priming exist (Obura et al., 2021, Abdulkareem et al., 2024, Berchie et al., 2010), few have examined genotype-specific responses to hydropriming under controlled conditions. This is a critical knowledge gap given that BGN is predominantly cultivated as landraces, with no commercially standardised varieties currently available. Applying a one-size-fits-all priming protocol may therefore overlook important variations in the seed coat permeability, metabolic activation, and emergence rates among landraces.

This study investigates the effects of hydropriming on the germination, emergence, and early seedling growth across four BGN landraces by evaluating key physio-logical and morphological parameters, including the days to emergence, shoot and root length, leaf development, biomass accumulation, and root-to-shoot ratio. This research aims to identify the optimal priming durations for enhancing early vigour. The findings will contribute to developing cost-effective and scalable seed enhancement practices that support the broader adoption of Bambara groundnut in climate-smart agricultural systems, particularly in drought-prone and resource-constrained environments.

5.2. Materials and Methods

5.2.1. Plant Material

Four BGN landraces (Nov4, NW, ARC, and 519) were selected for this study. All seeds were obtained from the University of KwaZulu-Natal's Bambara groundnut germplasm collection. To ensure uniform germination and minimise variation due to environmental history, seeds were harvested during the same growing season and stored under controlled ambient conditions until use.

5.2.2. Seed Priming and Sowing

Hydropriming was conducted by soaking seeds in distilled water at room temperature for 0 (unprimed control), 12, 24, or 36 h. After soaking, seeds were blotted with paper towels and air-dried for two hours at room temperature to remove surface moisture. Primed seeds were sown directly into 8-litre (L) thermoform pots filled with Gromor Potting Mix (30 dm^3 per pot), a commercially available sterile medium. This substrate was selected to ensure consistency in the texture, drainage, and nutrient baseline across all experimental units. Sowing was conducted immediately after the 2-hour drying period to maintain seed viability and ensure treatment consistency. All pots were watered with 250 mL of water before sowing to establish a uniform starting condition. The frequency was determined gravimetrically by maintaining field capacity through weight monitoring, precision digital weighing scale (±0.01 g).

5.2.3. Experimental Design and Greenhouse Conditions

The experiment was conducted under greenhouse conditions at the Controlled Research Facility (CERU), University of KwaZulu-Natal, Pietermaritzburg, South Africa (29°37′37.5″ S; 30°24′10.4″ E). The greenhouse maintained a mean air temperature of 25 ± 2 °C and a relative humidity of 60 ± 3%.

The experimental design was a 4 × 4 factorial completely randomised design (CRD), consisting of four landraces and four priming durations. Each treatment combination was replicated three times, with five seeds per pot, resulting in a total of 48 experimental units. Pots were arranged randomly on raised benches and irrigated with 250 mL of tap water every two days. Watering frequency was adjusted based on visual inspection of moisture levels to prevent both drought stress and over-saturation.

5.2.4. Emergence Assessment

Emergence was monitored daily and defined as the visible appearance of the hypocotyl above the soil surface. Days to 50% emergence were calculated per pot to evaluate uniformity across treatments.

5.2.5. Water Imbibition

The water uptake capacity during priming was assessed using a digital precision balance (±0.01 g). For each priming interval (0, 12, 24, 36 h), five seeds per landrace were weighed before and after priming. Seeds were gently blotted before final weighing to remove excess surface water. The imbibition percentage was calculated using Equation (5.1):

$$\text{Water imbibition (WI)} = \frac{\text{WSAP} - \text{WSBP}}{\text{WSBP}} \times 100 \tag{5.1}$$

where WSAP is the weight of the seed after priming; WSBP is the weight of the seed before priming.

5.2.6. Seedling Growth and Morphological Measurements

At 30 days after sowing (DAS), three seedlings per pot were randomly selected and sampled for morphological and biomass analysis. The shoot length was measured from the base of the stem to the tip of the longest leaf; the root length was measured from the stem base to the tip of the longest root after gentle washing. Leaf number and length (longest leaf per seedling) were also recorded.

Preliminary observations were made at 28 DAS to assess developmental uniformity, but all final measurements and data reported were standardised to 30 DAS.

5.2.7. Root and Shoot Biomass Allocation

Shoots were separated from roots by cutting at 5 cm above soil level. Roots were washed with distilled water to remove soil residue. Shoot and root components were oven-dried at 60 °C for 48 h. Dry weights were recorded using an analytical balance (±0.001 g).

The root mass ratio (RMR), shoot mass ratio (SMR), and root-to-shoot ratio (RSR) were calculated using Equations (5.2)–(5.4):

$$\text{Root mass ratio} = \frac{\text{Dry mass of root}}{\text{Total dry mass of plant}} \tag{5.2}$$

$$\text{Shoot mass ratio} = \frac{\text{Dry mass of shoot}}{\text{Total dry mass of plant}} \tag{5.3}$$

$$\text{Root shoot ratio} = \frac{\text{Root dry mass}}{\text{Shoot dry mass}} \tag{5.4}$$

5.2.8. Statistical Analysis

All statistical analyses were performed using Genstat 23rd Edition (VSN International, Hemel Hempstead, UK). Two-way ANOVA was applied to evaluate the effects of the genotype, the priming duration, and their interaction. Treatment means were separated using Fisher's protected least significant difference (LSD) test at the 5% significance level.

Multivariate analysis was conducted using OriginPro 2025 (OriginLab Corp., Northampton, MA, USA). Principal component analysis (PCA) and Pearson correlation analysis were performed on standardised, averaged trait values for each genotype × priming duration combination (n = 16) in order to explore trait co-variation patterns and genotype-specific responses to priming. Results were visualised using biplots and correlation heatmaps.

5.3. Results

5.3.1. Imbibition Responses of BGN Genotypes

The genotypes displayed distinct water uptake patterns in response to the increasing priming durations (Figure 5.0.1; Table 5.0.1). Genotype 519 exhibited the fastest and most pronounced hydration rate, with the seed weight increasing from 0.6884 g (unprimed) to 1.366 g after 36 h of hydropriming. Correspondingly, the water imbibition for 519 rose from 8.72% to 17.31%, the highest among all the genotypes evaluated. This rapid and sustained uptake suggests superior seed coat permeability or internal mechanisms facilitating water absorption, making 519 a highly responsive candidate for priming interventions. Genotype NW, in contrast, showed the slowest water uptake, with the seed weight rising from 0.794 g to 1.0608 g over 36 h, and a corresponding water imbibition increase from 10.11% to 13.51%. ARC and Nov4 demonstrated moderate water absorption capacities. ARC recorded a final weight of 1.0734 g and an imbibition of 11.5% at 24 h, while Nov4 increased from 4.93% to 11.10% over the priming period, despite starting with the lowest initial water uptake. The delayed but sharp increase in Nov4 suggests that extended priming durations may be essential to overcome the physiological dormancy or hard seed characteristics in certain genotypes. Overall, these results reveal genotype-specific differences in the hydration capacity and responsiveness to hydropriming. Such variation has practical implications for seed management strategies, as selecting genotypes like 519 could enhance uniform emergence, particularly under water-limited conditions. Meanwhile, slower-imbibing types such as Nov4 may benefit from extended priming durations to optimise field establishment.

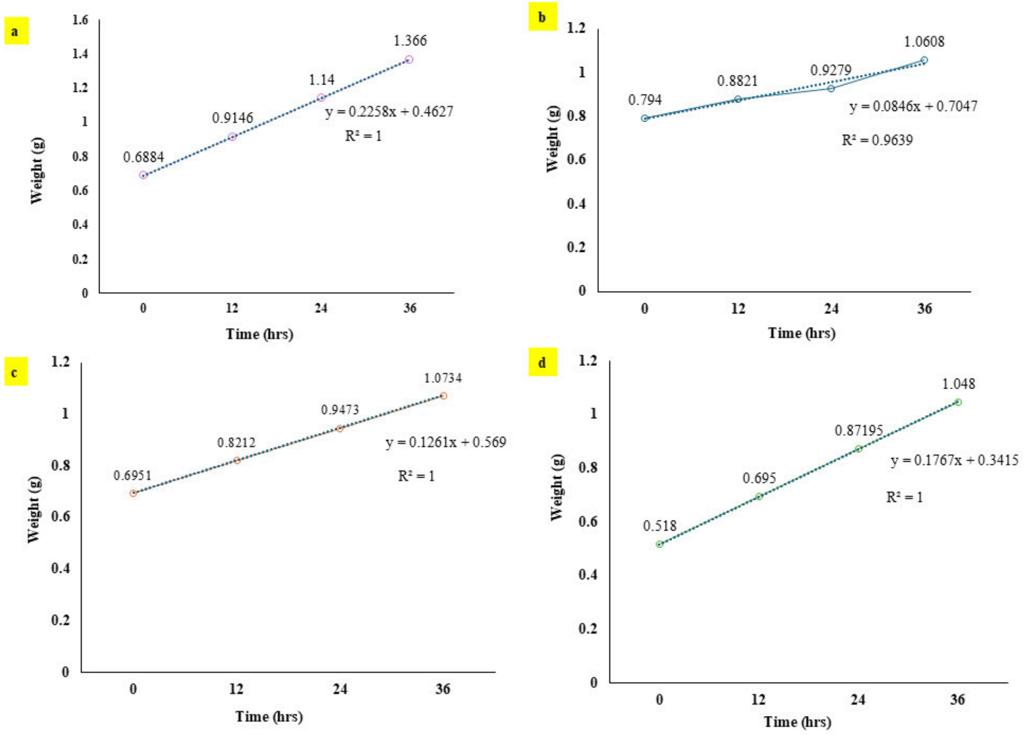

Figure 5.0.1: Effect of hydropriming duration on imbibition rate across six Bambara groundnut landraces : (a) 519, (b) NW, (c) ARC, and (d) Nov4

Table 5.0.1: Water imbibition (%) of BGN genotypes at different priming durations (0–36 h).

Genotype	**0**	**12**	**24**	**36**
ARC	10.5	10.7	11.5	13.5
519	8.7	11.6	14.5	17.3
NW	10.1	11.2	11.8	13.5
Nov4	4.9	5.9	6.6	11.1

Water imbibition (%) was calculated from Equation (1), where WSBP is the initial seed weight before priming and WSAP is the seed weight after the respective priming duration. Values represent the means of replicates. For duplicate time points, average values were used.

5.3.2. Effects of Priming Duration on Seedling Growth of BGN Genotypes

Seedling growth responses varied significantly with both genotype and priming duration, showing a clear interaction pattern. As priming duration increased, all genotypes exhibited progressive improvements in shoot and root development, but the magnitude of response differed among them (Figures 5.0.2–5.0.4). Unprimed controls displayed slow emergence and weak seedling establishment, characterised by shorter shoots and limited root elongation. A 12-hour priming period produced moderate gains in seedling vigour, while 24-hour treatments markedly enhanced root and shoot elongation, indicating improved metabolic activation and reduced dormancy effects.

At 36 hours, seedlings of all genotypes showed vigorous growth with taller shoots, broader leaves, and increased root biomass. The genotypic responses, however, revealed distinct physiological strategies: Genotype 519 demonstrated the strongest response to prolonged priming, suggesting a highly permeable seed coat and efficient reactivation of enzymatic and hormonal processes that support rapid growth. In contrast, ARC and Nov4 exhibited more conservative hydration responses, likely due to thicker or less permeable seed coats that slow water uptake and delay metabolic reactivation. NW displayed intermediate behaviour, balancing hydration efficiency with sustained seedling vigour.

These interaction trends highlight the role of inherent seed coat traits in mediating the physiological response to priming. The observed improvements in root and shoot growth at longer priming durations reflect enhanced mobilisation of seed reserves, faster cell expansion, and improved water relations traits that collectively contribute to early establishment and potential drought resilience in field conditions.

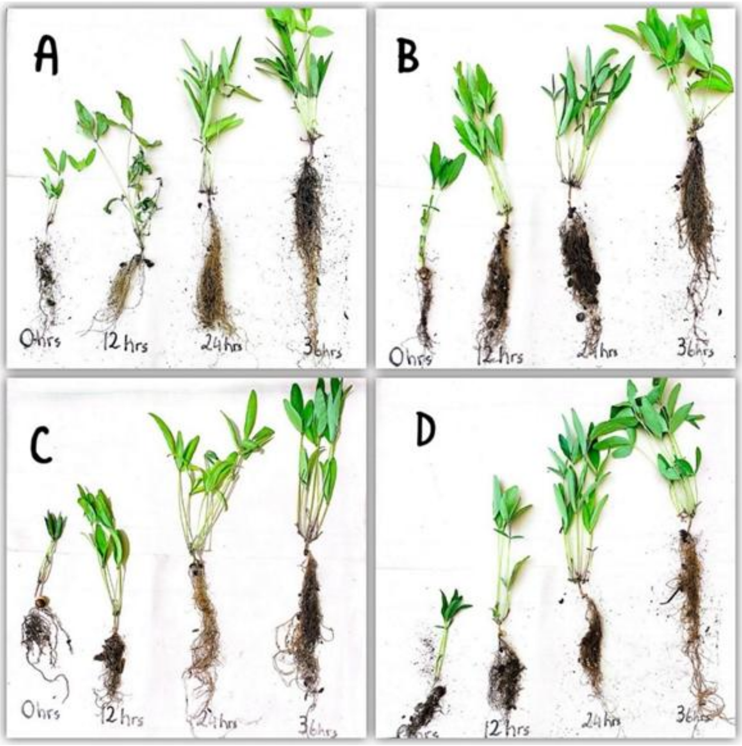

Figure 5.0.2: Bambara seeds that were primed for 0, 12, 24, and 36 h. (A) Nov4, (B) NW, (C) ARC, and (D) 519

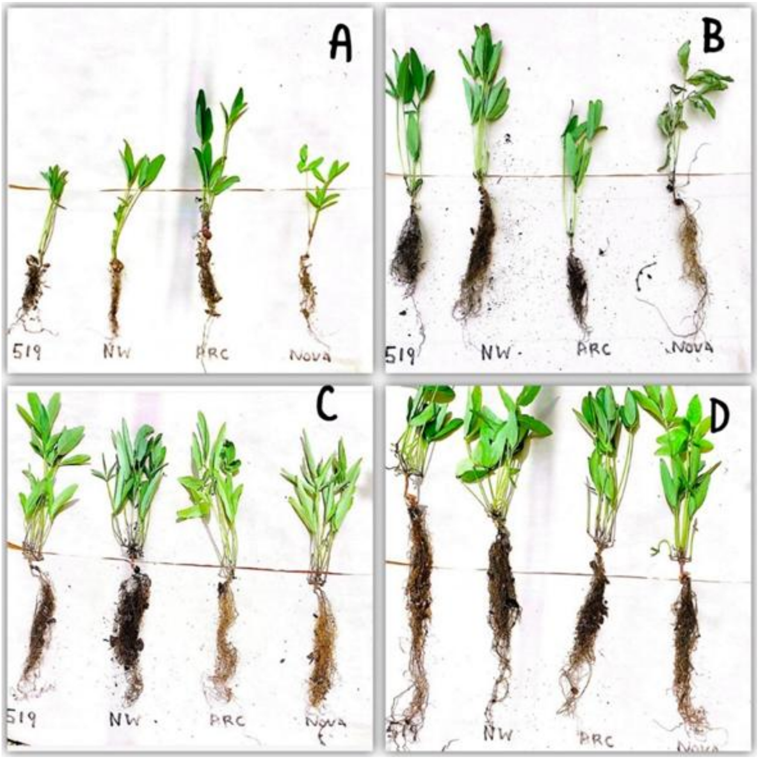

Figure 5.0.3: Bambara landraces (519, NW, ARC, and Nov4) primed for different hours. (A) 0 h, (B) 12 h, (C) 24 h, and (D) 36 h.

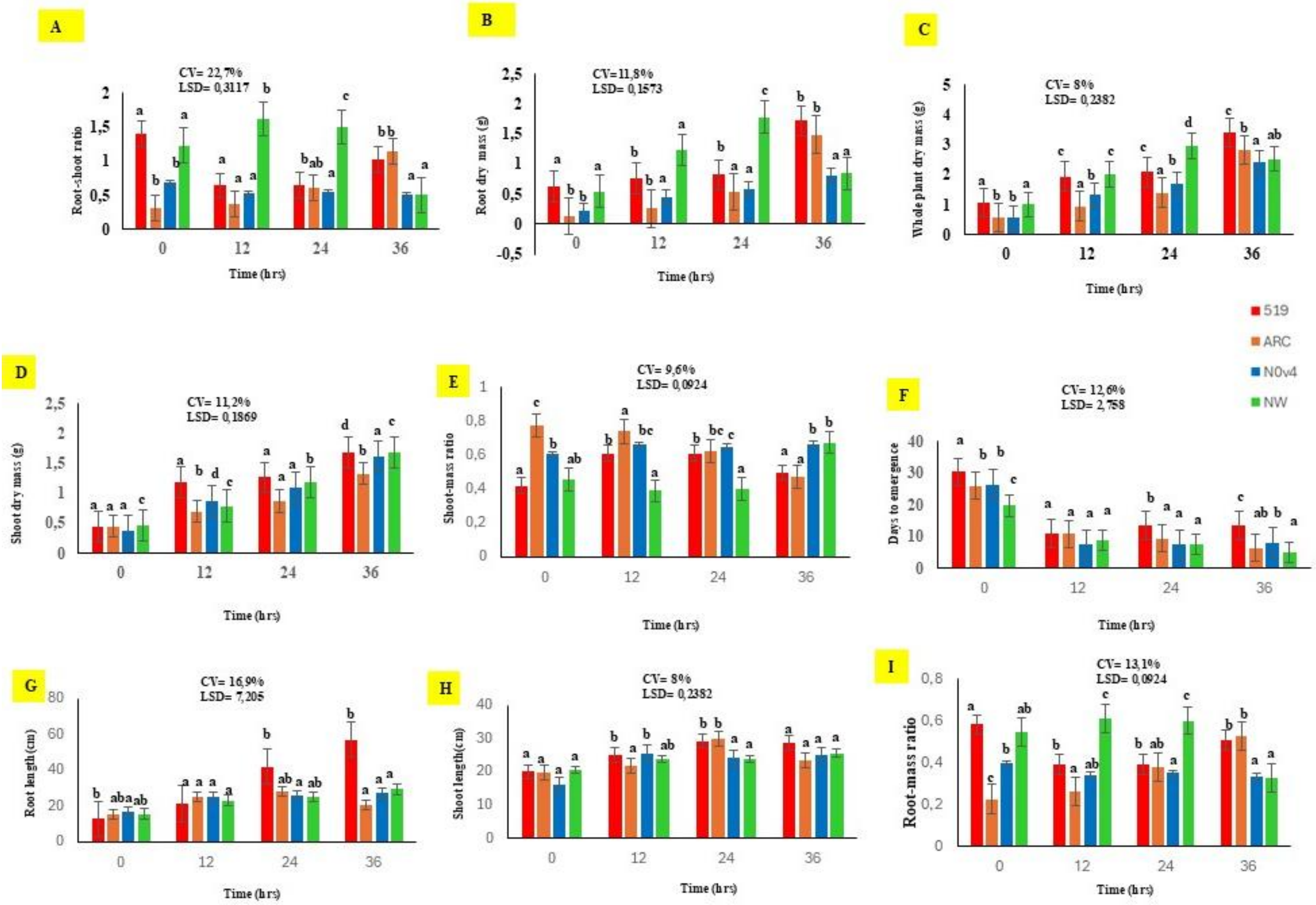

Figure 5.0.4: Effects of genotype (G), priming time (T), and their interaction (G × T) on key plant traits: root-to-shoot ratio (A), root dry mass (B), whole-plant dry mass (C), shoot dry mass (D), shoot mass ratio (E), days to emergence (F), root length (G), shoot length (H), and root mass ratio (I). Data are presented as means ± standard error (SE), based on three biological replicates. Bars sharing the same letter are not significantly different according to Fisher's least significant difference (LSD) test ($p < 0.05$); bars with different letters indicate statistically significant differences between treatment means. Error bars represent the standard error of the mean.

Quantitative data confirmed these visual trends. The analysis of variance (Table 5.0.2; Figure 5.0.4) showed that the genotype (G) significantly affected the days to 50% emergence (DE) ($p < 0.01$), root length (RL) ($p < 0.01$), and whole-plant dry mass (WPDM) ($p < 0.01$). The priming time (T) significantly influenced the DE, shoot length (SL), root length (RL), and shoot dry mass (SDM), all with $p < 0.01$. The G × T interaction also significantly influenced the root dry mass (RDM), shoot mass ratio (SMR), and root mass ratio (RMR). The bars in Figure 5.0.4 are labelled with letters indicating statistically grouped means; identical letters represent no statistically significant difference. The sample size for each treatment was n = three pots, with three seedlings sampled per pot.

Table 5.0.2: Analysis of variance showing mean squares and significant tests of key plant traits when primed at different time intervals

Source of Variation	df	DE	SL	RL	LL	RFM	SFM	WPFM	RDM	SDM	WPDM	RSR	SMR	RMR
Genotype (G)	3	98.139 **	19.833 *	315.50 **	3.951 **	1.970 **	15.419 **	18.072 **	0.957 **	0.195 **	1.728 **	1.108 **	0.086 **	0.086 **
Time (T)	3	831.694 **	141.722 **	807.93 **	13.076 **	8.802 **	18.757 **	52.598 **	1.523 **	2.739 **	8.322 **	0.035 *	0.003 NS	0.003 NS
G × T	9	11.083 *	16.037 *	221.37 **	1.001 *	0.679 **	1.394 **	1.593 **	0.463 **	0.039 *	0.408 **	0.518 **	0.044 **	0.044 **
Residual	32	2.750 NS	6.963 NS	18.77 NS	0.322 NS	0.012 NS	0.062 NS	0.067 NS	0.009 NS	0.013 NS	0.021 NS	0.035 NS	0.003 NS	0.003 NS

df: degrees of freedom; NS: not significant. * $p < 0.05$; ** $p < 0.01$. Emergence (DE), shoot length (SL), root length (RL), leaf length (LL), root fresh mass (RFM), shoot fresh mass (SFM), whole-plant fresh mass (WPFM), root dry mass (RDM), shoot dry mass (SDM), whole-plant dry mass (WPDM), root shoot ratio (RSR), shoot mass ratio (SMR), and root mass ratio (RMR).

5.3.3. Principal Component Analysis (PCA)

Table 5.0.3 and Figure 5.0.5 present the results of the principal component analysis (PCA), which was used to examine the trait co-variation in response to the hydro-priming durations. At all the time points, PC1 explained the largest proportion of the total variation, ranging from 53.2 – 60.3 %, and was strongly influenced by traits related to biomass accumulation and partitioning namely, the whole-plant dry mass (WPDM), root-to-shoot ratio (RSR), root dry mass (RDM), and shoot length (SL). This indicates that these traits are the most responsive to priming and are key indicators of the early seedling growth performance across genotypes. The PCA biplots revealed distinct clustering patterns, highlighting genotype-specific trait associations. Genotype 519 consistently aligned with the WPDM, shoot dry mass (SDM), and leaf length (LL), especially under 24 h of priming, suggesting that this genotype may exhibit greater biomass allocation and canopy development under extended priming conditions. NW grouped closely with the root fresh mass (RFM) and shoot mass ratio (SMR), indicating a stronger allocation to shoot structures relative to the total mass. ARC was more closely associated with the RSR and root mass ratio (RMR), pointing to a tendency for root-biased biomass distribution. In contrast, Nov4 showed limited associations with the key growth traits across the priming durations, suggesting a relatively weaker or less distinct response to priming. These genotype-specific associations provide insights into how each landrace responds physiologically to hydropriming, reinforcing the value of tailoring priming protocols to specific genetic backgrounds. Overall, the PCA highlights the WPDM, RDM, and SL as consistent indicators of the seedling performance and responsiveness to priming.

Table 5.0.3: Summary of factor loadings, eigenvalue measures of sampling adequacy, and percent and cumulative variation for plant traits.

	0 h			**12 h**			**24 h**			**36 h**		
Variables	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
WPDM	0.328	−0.170	−0.035	0.318	−0.193	0.107	0.372	0.073	0.118	0.372	0.073	0.118
RSR	0.285	−0.269	−0.167	0.300	−0.032	−0.313	0.324	−0.244	0.023	0.324	−0.244	0.023
RDM	0.310	−0.219	−0.110	0.331	−0.098	−0.134	0.369	−0.101	0.091	0.369	−0.101	0.091
SL	0.286	0.131	0.370	0.035	−0.550	0.134	0.204	0.381	0.181	0.204	0.381	0.181
RL	−0.306	−0.150	0.274	−0.269	0.022	−0.399	0.263	0.311	0.232	0.263	0.311	0.232
WPFM	0.308	0.236	−0.001	0.332	0.120	0.099	0.265	0.221	−0.438	0.265	0.221	−0.438
LL	0.293	0.227	0.219	0.193	0.437	−0.189	0.005	0.436	−0.294	0.005	0.436	−0.294
RFM	0.283	−0.251	0.222	0.308	−0.253	−0.001	−0.274	0.229	0.398	−0.274	0.229	0.398
SFM	0.191	0.414	−0.128	0.297	0.262	0.128	0.271	0.204	−0.445	0.271	0.204	−0.445
DE	0.026	0.247	−0.633	0.042	0.385	0.463	0.265	0.174	0.497	0.265	0.174	0.497
SMR	−0.254	0.322	0.186	−0.312	0.099	0.247	−0.331	0.229	−0.054	−0.331	0.229	−0.054
RMR	0.254	−0.322	−0.186	0.312	−0.099	−0.247	0.331	−0.229	0.054	0.331	−0.229	0.054

SDM	0.272	0.172	0.383	0.102	−0.272	0.530	−0.039	0.464	0.059	−0.039	0.464	0.059
Eigenvalue	8.216	3.894	1.891	8.447	3.129	2.425	6.911	4.571	1.518	6.911	4.571	1.518
Variability (%)	58.685	27.811	13.504	60.332	22.350	17.318	53.163	35.162	11.675	53.163	35.162	11.675
Cumulative (%)	58.685	86.496	100	60.332	82.682	100	53.163	88.325	100	53.163	88.325	100

DE: days to emergence; SL: shoot length; RL: root length; LL: leaf length; RFM: root fresh mass; SFM: shoot fresh mass; WPFM: whole-plant fresh mass; RDM: root dry mass; SDM: shoot dry mass; WPDM: whole-plant dry mass; RSR: root shoot ratio; SMR: shoot mass ratio; RMR: root mass ratio.

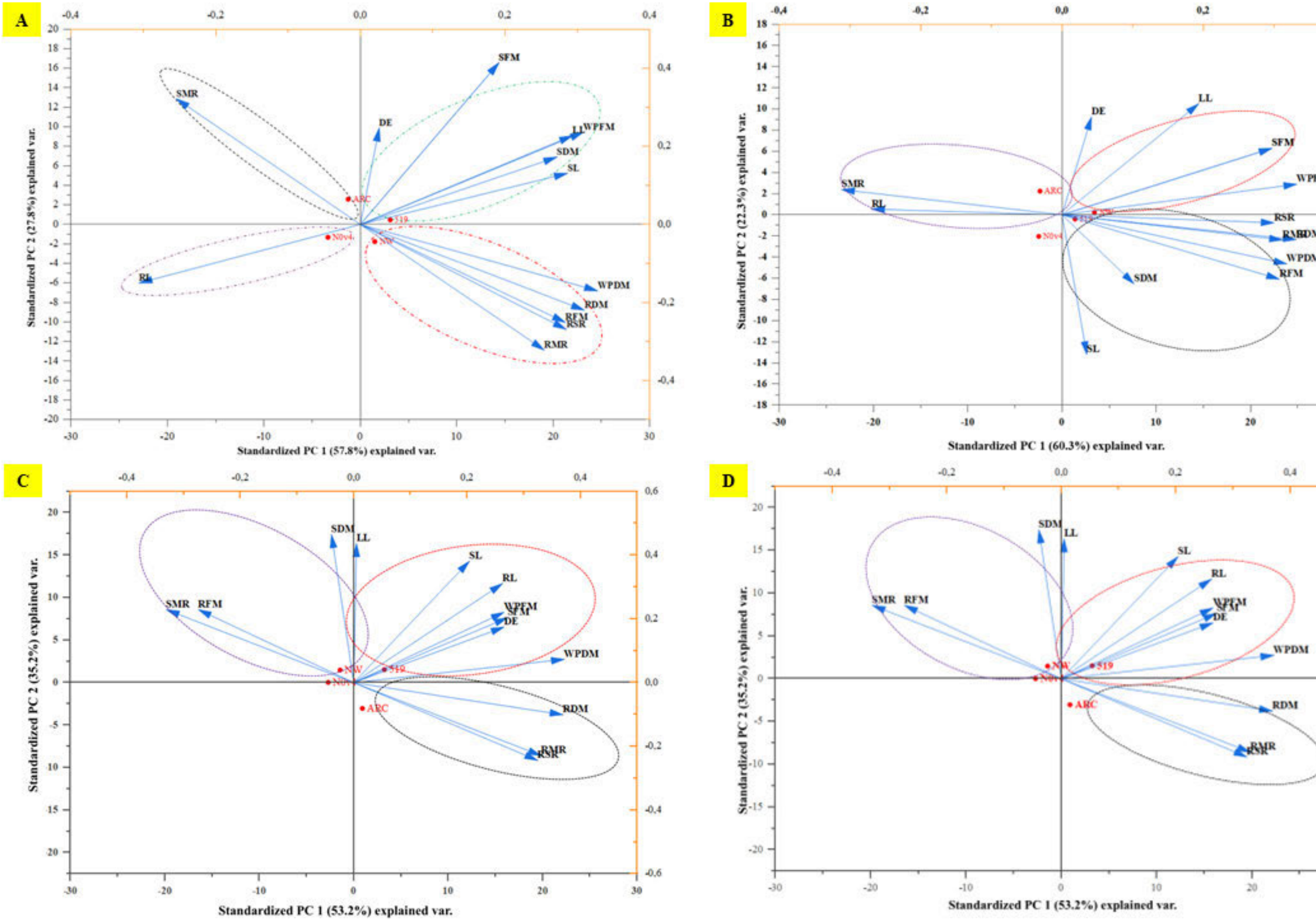

Figure 5.0.5: Principal component (PC) biplots demonstrating the relationships among plant traits of four Bambara genotypes (ARC, Nov4, 519, and NW) primed at different prime intervals: (A) 0 h, (B) 12 h, (C) 24 h, and (D) 36 h.

5.3.4. Pearson Correlation Analysis

The Pearson correlation analysis (Figure 5.0.6) revealed strong and consistent relationships among the traits related to biomass partitioning and overall plant development across all the priming durations. The whole-plant dry mass (WPDM) was positively and significantly correlated with the root dry mass (RDM) and root-to-shoot ratio (RSR) ($r = 1.0$, $p < 0.001$), indicating that the plants with higher total biomass also tended to invest proportionally more in root structures. This suggests that hydropriming, particularly at longer durations, may support balanced growth and improved root development, which are important for early establishment and resilience under water-limited conditions

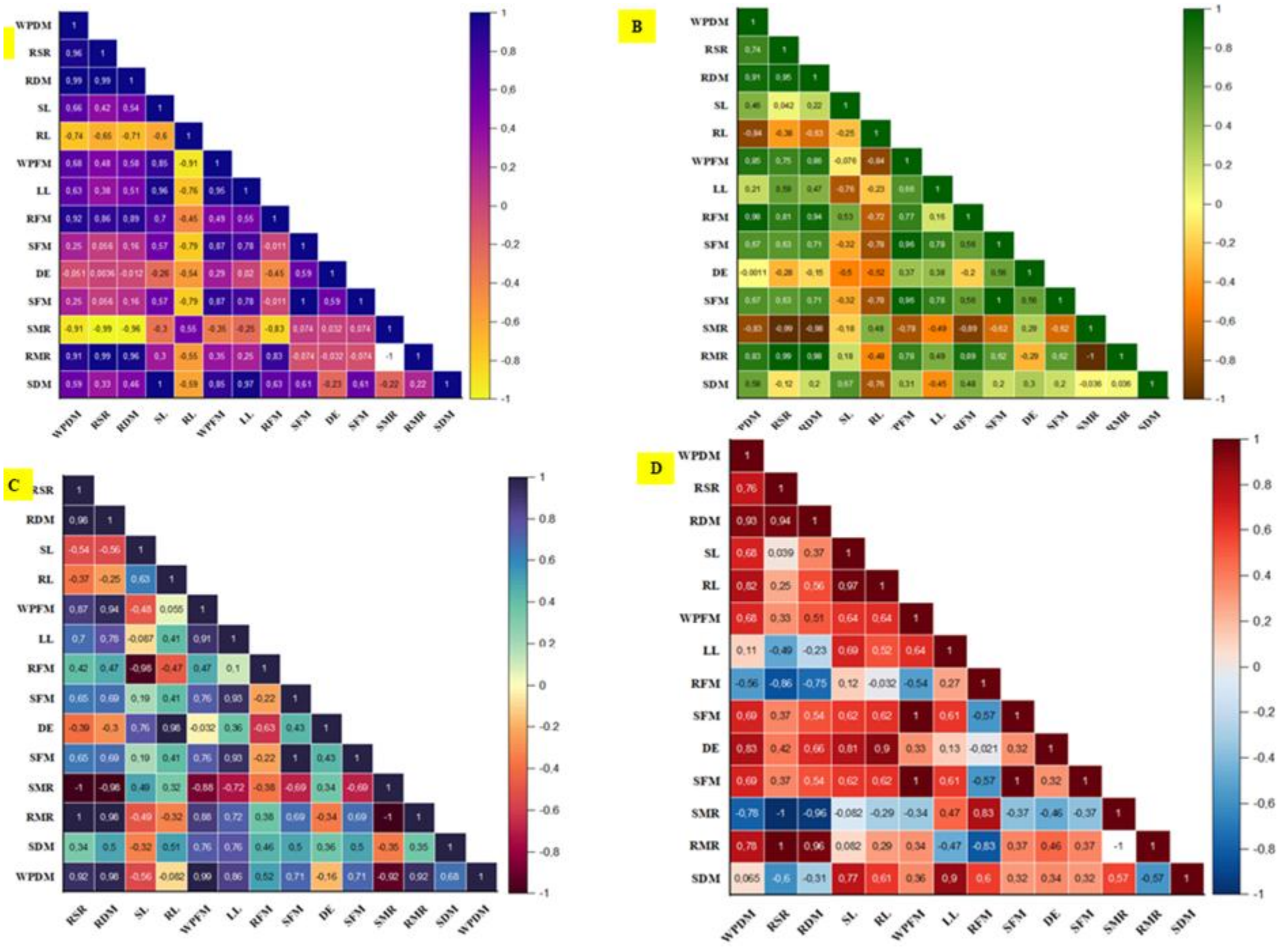

Figure 5.0.6: Pearson correlation coefficients showing relationships between plant traits and priming times (A) 0 h, (B) 12 h, (C) 24 h, and (D) 36 h: days to emergence (DE), shoot length (SL), root length (RL), leaf length (LL), root fresh mass (RFM), shoot fresh mass (SFM), whole-plant fresh mass (WPFM), root dry mass (RDM), shoot dry mass (SDM), whole-plant dry mass (WPDM), root shoot ratio (RSR), shoot mass ratio (SMR), and root mass ratio (RMR).

In contrast, the shoot mass ratio (SMR) showed a strong negative correlation with both the RDM and RSR, reflecting the trade-off between shoot dominance and root development. This inverse relationship suggests that genotypes or treatments promoting greater root allocation may do so at the expense of the shoot mass proportion, highlighting distinct biomass partitioning strategies among landraces. While some correlations such as those between the derived ratios and their component traits were expected due to mathematical relationships, their consistent direction and strength across the priming durations underscore the stability of these patterns. These findings contribute to identifying reliable physiological indicators of the seedling performance under hydropriming and offer a basis for the future trait-based screening of responsive genotypes.

5.4. Discussion

Seed imbibition is the initial and critical phase of germination (Bradford, 2017) , triggering metabolic reactivation and influencing the subsequent seedling performance (Louf et al., 2018). In this study, the BGN genotypes exhibited distinct and statistically significant variations in their water uptake across the priming durations, reaffirming the importance of genotype-specific physiological traits in early-stage seed responses.

Genotype 519 demonstrated the highest water imbibition, increasing from 8.72% at 0 h to 17.31% at 36 h, alongside a final seed weight of 1.366 g. This steep hydration gradient likely reflects a superior seed coat permeability or heightened metabolic predisposition to absorb water (Upretee et al., 2024). Conversely, NW, despite having the highest initial seed weight (0.794 g), showed the slowest imbibition trajectory, culminating in 13.51% at 36 h. This more controlled water uptake pattern suggests a less permeable seed coat, which may serve as a buffering mechanism to mitigate imbibitional injury, especially under fluctuating moisture conditions (Mandizvo and Odindo, 2019). Landrace ARC and Nov4 exhibited moderate hydration responses, with Nov4 showing the lowest initial uptake but a marked increase by 36 h. These observations align with earlier reports linking seed coat composition, porosity, and dormancy traits to differential water uptake in legumes (Kumeera et al., 2018, Perera et al., 2023, Sofi et al., 2022). It is important to note, however, that the initial seed weights used for hydration varied among the genotypes, while the same volume of water was applied across the treatments. This could introduce unequal seed-to-water ratios, which may have influenced the imbibition rates and hydration efficiency. Although consistent volumes were maintained, future studies should standardise the substrate-to-solvent ratio either by weight or volume to ensure fairer comparisons and a more robust interpretation of the water uptake dynamics.

Interestingly, rapid hydration in genotype 519 did not translate to the fastest emergence. Despite its high water uptake, 519 exhibited delayed emergence, potentially due to imbibitional stress or asphyxiation from rapid water entry limiting the oxygen availability to the embryo (Singh et al., 2018, Cheng et al., 2017, Kostoláni et al., 2021). This paradox highlights that faster water uptake does not always equate to an improved early performance. In contrast, NW's slower but steady imbibition may have allowed for a more regulated activation of enzymatic and metabolic pathways, resulting in earlier and more uniform emergence(Ali et al., 2005). These genotype-specific dynamics underscore the importance of balancing the hydration rate with metabolic coordination to optimise germination outcomes.

The priming duration emerged as a critical determinant of seedling development across all the genotypes. While unprimed seeds consistently showed poor shoot and root development, notable improvements were observed at 24 and 36 h. These durations appeared to facilitate the uniform hydration and physiological activation necessary for robust seedling establishment. These findings align with previous studies showing that hydropriming initiates enzymatic activity, repairs oxidative damage, and promotes embryo elongation (Waqas et al., 2019, Zaman et al., 2017).

Visual and quantitative assessments revealed genotype-specific responses to priming. At 36 h, genotypes 519 and NW exhibited the strongest seedling performances, characterised by greater shoot heights, root biomasses, and whole-plant dry masses. ARC and Nov4 responded positively, though to a lesser degree. These differences may reflect intrinsic genetic variation in the seed vigour, metabolic capacity, or responsiveness to hydration stimuli, as similarly observed in chickpea, soybean, and other legume crops (Sajjan et al., 2017, Antunes et al., 2021, Ghassemi-Golezani, 2008).

The ANOVA results confirmed that the interaction (G × T) significantly influenced key seedling traits. The genotype had a strong effect on the root length, whole-plant dry mass (WPDM), and root-to-shoot ratio (RSR) ($p < 0.01$), while the priming time significantly influenced the days to 50% emergence (DE), shoot length (SL), and shoot dry mass (SDM) ($p < 0.01$). The significant G × T interaction effects observed for the root dry mass (RDM), shoot mass ratio (SMR), and root mass ratio (RMR) suggest that priming outcomes are not only time-dependent but also genotype-specific. This supports the need for customised priming protocols to enhance early seedling vigour under diverse environmental conditions, especially in water-limited settings (Bester et al., 2024).

Principal component analysis (PCA) provided further insight into the trait coordination and genotype performance under different priming durations. PC1 consistently accounted for the majority of the variance (>50%) and was primarily influenced by traits linked to biomass accumulation (e.g., WPDM, RDM, SL, RSR). Genotype 519 clustered closely with the WPDM and SDM at 36 h, indicating high biomass investment under prolonged priming. NW associated more with the SMR and RFM, while ARC aligned with the RSR and RMR, revealing differing allocation strategies among the genotypes. These patterns support findings that suggest that seed priming can influence biomass partitioning and shape early developmental trajectories (Xie et al., 2016, Bhowmick et al., 2013, Shariatmadari et al., 2017). The correlation analysis reinforced these relationships. The WPDM was positively correlated with the RDM and RSR, suggesting that the coordinated allocation of resources toward root development enhances overall vigour (Yin et al., 2019, Monson et al., 2022). The expected negative correlations between the SMR and both the RDM and RSR reflect trade-offs in the allocation between the shoot and root compartments and further highlight the strategic adjustments induced by priming.

Taken together, the findings of this study demonstrate that BGN genotypes vary in their physiological responses to hydropriming. Longer priming durations, particularly 36 h, generally showed potential in promoting seedling vigour. However, the extent of the benefit was genotype dependent. Optimising priming for each genotype based on their imbibition behaviour, emergence timing, and trait performance can inform scalable seed enhancement strategies. These findings offer a starting point for practical implications to improving BGN establishment in semi-arid and climate-vulnerable regions, where early crop establishment is critical for yield resilience and food security.

5.5. Conclusions

This study demonstrates the effectiveness of hydropriming as a low-cost, pre-sowing intervention to enhance the early seedling performance in Bambara groundnut (BGN). Significant improvements in the shoot elongation, root development, and whole-plant biomass were observed across the genotypes, particularly at a priming duration of 36 h. Genotypes 519 and NW exhibited the most pronounced responses to extended priming, underscoring their suitability for seed enhancement strategies aimed at improving early vigour in water-limited environments. The water imbibition patterns varied significantly among the genotypes, with 519 showing the fastest hydration rate but delayed emergence, while NW demonstrated slower yet more regulated water uptake and earlier emergence. These differences highlight the importance of aligning the priming duration with genotype-specific physiological traits to avoid imbibitional injury and maximise seedling establishment.

Multivariate analyses further revealed that traits such as the root-to-shoot ratio (RSR), root dry mass (RDM), and whole-plant dry mass (WPDM) were key contributors to early vigour under priming conditions. The strong associations between these traits and the seedling performance support the utility of trait-based approaches in selecting genotypes for priming optimisation. Hydropriming for 36 h appears to be a promising and scalable approach for smallholder farmers, particularly in semi-arid and resource-constrained regions where rapid and uniform crop establishment is essential. However, the findings are based on controlled greenhouse experiments, and broader applicability requires validation under field conditions.

Future research should prioritise multi-location field trials, integration with diverse agroecological zones, and in-depth physiological and biochemical profiling to better understand the mechanisms underlying genotype-specific priming responses. Also, further studies exploring hydropriming durations beyond 36 hours was added to the conclusionSuch work will contribute to developing climate-resilient seed systems and support the broader adoption of underutilised legumes like Bambara groundnut for improved food and nutritional security in sub-Saharan Africa.

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Chapter 6: SUMMARY, CONCLUSIONS AND RECOMMENDATIONS

6.1 Summary

This thesis set out to investigate the adaptive capacity of *Bambara groundnut (Vigna subterranea L. Verdc.)* and its potential contribution to advancing climate-smart agriculture (CSA) in sub-Saharan Africa. Through three interconnected studies focusing on root system architecture, seed coat traits, and seed priming responses. The thesis added to the body of knowledge on the physiological and structural mechanisms that underpin early-stage drought resilience. Collectively, the studies addressed key gaps identified in the literature concerning below-ground traits, seed coat functionality, and genotype-specific management interventions for this underutilised legume.

The root phenotyping study demonstrated that *Bambara groundnut* exhibits considerable genotypic variation in root system architecture (RSA) traits such as root depth, lateral spread, and dry mass. These differences were found to directly influence the plant's ability to access soil moisture and sustain growth under water-limited conditions. Genotypes with deeper and more extensive root systems showed superior drought avoidance capacity, highlighting their potential as parental material for breeding programmes targeting marginal, low-input production environments. The results underscore the importance of RSA as a critical component of drought resilience and provide measurable selection criteria for participatory and decentralised breeding approaches.

The second experiment on seed coat morphology and physiology established that traits such as coat thickness, pigmentation, and permeability significantly influence water uptake dynamics and the risk of imbibitional injury during germination. The study revealed a physiological trade-off between mechanical protection and rapid hydration—thicker, darker coats offered better protection against solute leakage but delayed imbibition, while thinner coats facilitated faster water uptake but increased susceptibility to stress. Importantly, certain genotypes exhibited adaptive combinations of these features, suggesting that the relationship between seed coat structure and germination efficiency is not strictly linear. These findings advance understanding of how physical and physiological seed traits interact to determine germination success, particularly under erratic rainfall and variable soil moisture conditions typical of smallholder farming systems.

The hydropriming study built upon these insights by testing a simple, farmer-friendly intervention designed to improve germination and early seedling growth. The results confirmed that hydropriming substantially enhanced emergence, shoot elongation, and biomass accumulation when tailored to genotype-specific hydration responses. A 36-hour priming duration produced the most consistent improvements across genotypes, providing a low-cost and scalable technique to promote rapid and uniform crop establishment in rainfed environments. However, variation among genotypes highlighted the need for optimisation to prevent imbibitional injury in more sensitive landraces. This work positions hydropriming as a practical tool for improving establishment success and early vigour, contributing to the broader goal of enhancing resilience in resource-constrained production systems.

Viewed together, these three studies provide an integrated understanding of Bambara groundnut adaptation to water stress across complementary biological scales. Root system architecture ensures sustained access to deep soil moisture, seed coat properties regulate the timing and efficiency of water uptake, and priming acts as a physiological trigger that enhances early growth and vigour. This continuum, from structural to physiological adaptation, illustrates how early-stage traits interact to influence drought resilience, establishing a trait-based framework for improving Bambara groundnut through both breeding and agronomic management. The findings reaffirm the crop's potential as a cornerstone of climate-smart agriculture by combining inherent drought tolerance with responsiveness to simple, accessible management interventions.

6.2 Conclusions

This research confirms that underutilised legumes, particularly Bambara groundnut, possess adaptive traits well suited to climate-smart agriculture in sub-Saharan Africa's water-limited environments. Through three interlinked studies, this thesis has generated new evidence on genotype-specific variation in root system architecture, seed coat traits, and seed priming responses. These findings contribute to a more rounded understanding of early-stage drought adaptation in a crop that lacks commercial varieties but holds substantial promise for resilient food systems.

The study demonstrated that root system architecture (RSA) varies significantly among landraces, with traits such as root depth, lateral spread, and dry mass serving as key indicators of drought avoidance. These traits provide practical selection criteria for participatory and decentralised breeding programmes, particularly those targeting low-input, smallholder production systems.

Seed coat morphology presented as an important determinant of germination performance and seedling vigour in Bambara groundnut. Variations in traits such as thickness, pigmentation, and structural permeability significantly influenced hydration movement, solute retention, and the risk of imbibitional injury during early germination. These findings show the physiological trade-off between mechanical protection afforded by thicker, pigmented coats and the rapid water uptake necessary for swift and uniform seedling emergence. This balance is particularly crucial in smallholder systems, where seeds are subject to variable storage conditions and unpredictable rainfall, making the selection of genotypes with optimal seed coat traits a key consideration for breeding programmes targeting climate-resilient crop establishment.

Hydropriming emerged as an effective, low-cost intervention for enhancing early seedling growth, particularly when tailored to the physiological traits of specific genotypes. The study showed that 36-hour priming significantly improved germination, shoot elongation, and biomass accumulation, offering a practical strategy for improving crop establishment in marginal environments. Its affordability and ease of implementation make it especially relevant for smallholder farmers with limited access to agro-inputs or irrigation.

Together, these findings support the repositioning of Bambara groundnut as a strategic crop for climate resilience. Its physiological plasticity and responsiveness to simple agronomic interventions offer clear opportunities for its integration into breeding pipelines, extension systems, and national climate-smart agriculture strategies.

6.3 Recommendations

Study limitations and future directions

While this study has produced important insights into the adaptive potential of Bambara groundnut, several limitations should be acknowledged. All experiments were conducted under controlled greenhouse conditions, which allowed for the isolation of genotype and treatment effects but do not fully replicate the complex, variable conditions found in smallholder fields. Therefore, field validation under diverse agroecological environments is essential to confirm the generalisability of these results.

The scope of the study was also limited to a relatively small number of landraces, six for root phenotyping, and five for seed coat and priming trials. While these genotypes offered meaningful contrasts, they do not capture the full extent of diversity within the broader Bambara groundnut germplasm. Future research should include a wider range of landraces to identify stable, widely adaptable traits and support breeding strategies that reflect regional seed preferences and agroecologies.

The research focused primarily on early growth stages: germination, emergence, and seedling development. Although critical for stand establishment, these traits must be linked to mid- and late-season performance to determine their true agronomic value. Follow-up studies should evaluate how early vigour translates into reproductive development, pod formation, and final yield under both stress and optimal conditions.

While the study demonstrated promising genotype-specific responses to hydropriming, root traits, and seed coat variability, these findings must be validated across seasons, soil types, and management systems. Multi-location trials, ideally integrated with participatory approaches involving farmers, would strengthen the relevance, applicability, and adoption of these interventions.

Future studies on Bambara groundnut under water stress could greatly benefit from incorporating stable carbon isotope analysis to provide deeper physiological insights into plant water-use dynamics. Environmental factors such as temperature, moisture, and atmospheric CO_2 concentration strongly influence photosynthetic processes, yet these were not explicitly quantified in the present study. Measuring carbon isotope discrimination (Δ) offers a robust and integrative approach to assess relative water use efficiency (WUE) across genotypes. Because atmospheric CO_2 consists predominantly of $^{12}CO_2$ ($\approx$99%) and a smaller fraction of $^{13}CO_2$ ($\approx$1%), plants discriminate against the heavier isotope during CO_2 fixation. This discrimination is greater in well-watered conditions, when stomata remain open, and decreases under drought stress as stomatal conductance declines. Consequently, Δ provides a reliable indicator of long-term WUE and photosynthetic performance. Future research should therefore explore carbon isotope discrimination as a complementary phenotyping tool for Bambara groundnut to identify landraces with superior WUE and adaptive photosynthetic responses under water-limited environments.

Contribution to knowledge and practice

Despite its limitations, this study makes an important contribution to the growing body of knowledge on climate-smart agriculture in sub-Saharan Africa. By focusing on Bambara groundnut, a neglected but resilient legume, it advances understanding of the physiological and morphological traits underpinning early drought adaptation in low-input farming systems. The identification of root traits linked to drought avoidance, seed coat characteristics affecting germination, and genotype-specific responses to hydropriming provides new insights for trait-based selection and agronomic management.

This research contributes to the broader agenda of repositioning underutilised crops as key assets in sustainable food systems. When supported by improved seed quality and targeted agronomic practices, Bambara groundnut has the potential to move from a subsistence crop to a commercially and ecologically valuable component of diversified, nutrition-sensitive agricultural systems. The findings offer practical implications for farmers, researchers, and policymakers working toward more inclusive and resilient food futures.

Research, agronomic, and policy recommendations

Future research could build on this foundation by incorporating advanced root phenotyping tools, such as digital imaging and modelling platforms, to quantify root traits with greater precision and scalability. The integration of molecular and genomic tools, including marker-assisted selection, would also support the identification of drought-resilient genotypes and speed up breeding progress. These efforts will be most effective when aligned with participatory breeding models that centre farmer knowledge and preferences.

Further investigation into the biochemical and structural basis of seed coat traits, particularly pigmentation, thickness, and permeability, is warranted. Such work could inform better post-harvest storage and seed quality assessment in informal seed systems. Practical guidelines should be developed to help farmers and seed producers distinguish between seed lots with superior traits, even without sophisticated infrastructure.

Given the positive results observed in this study, hydropriming should be promoted as a routine pre-sowing intervention for Bambara groundnut, particularly in drought-prone regions. Extension services and agricultural development programmes should be equipped to offer genotype-specific guidance, using accessible communication formats such as illustrated manuals, videos, and community-led demonstrations.

At the policy and institutional level, there is a need to formally recognise underutilised legumes, especially Bambara groundnut, in national seed catalogues, breeding agendas, and climate-smart agriculture frameworks. Investment should prioritise public research, seed system strengthening, and market development for these crops. Including Bambara groundnut in school feeding schemes, nutrition-sensitive programmes, and agroecological subsidy initiatives could help shift its perception from a ‘poor man’s crop’ to a climate-resilient, commercially viable alternative. Supporting community seed banks and local seed enterprises will be crucial to ensuring long-term access to quality seed and building resilient food systems in the face of climate change.