Trait Variation in Maize Across Social, Physiological, and Genetic Scales

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Abstract

Maize (*Zea mays* L.) is a key staple crop in Nigeria, underpinning household food security, dietary protein intake, and rural livelihoods. Despite its importance, productivity in rainfed systems is increasingly threatened by recurrent drought, while differences in the nutritional quality of commonly grown varieties remain poorly characterized within the context of farmer management and local environments. This thesis addresses these challenges through two interconnected studies.

The first study examined grain protein content and farmer varietal preferences in Ilorin South, Kwara State, Nigeria. Grain samples collected from smallholder farms were analyzed to compare three maize types: white, yellow, and red. Protein levels differed across both varietal type and location. Yellow maize generally recorded higher protein concentrations than white maize, whereas red maize showed intermediate values, indicating that both genetic background and growing conditions shape nutritional outcomes. A structured survey complemented the laboratory analysis by documenting farmer experiences with drought, seed sourcing, and cropping decisions. White maize was most widely cultivated, largely due to cultural and market preferences. Yellow maize also showed notable adoption, often associated with improved seed and perceived tolerance to dry conditions. Many farmers cultivated multiple varieties simultaneously as a strategy to reduce climate-related risk, and most relied on farm-saved seeds.

The second study evaluated drought response and plant–water relations in maize germplasm developed for genetic analysis. Five F_2 lines were grown under well-watered and water-limited treatments in controlled conditions. Water deficit reduced soil moisture and influenced key physiological traits, with significant variation observed among lines. Measurements of stomatal density, carbon isotope composition ($\delta^{13}C$), and intrinsic water-use efficiency suggested that internal physiological regulation, rather than stomatal number alone, was central to drought adaptation. Overall, the findings demonstrate that improving maize systems requires integrated attention to nutritional quality, genetic variation, environmental stress, and farmer decision-making.

1.0 General introduction

1.1 Background and Global Importance of Maize

Maize (*Zea mays* L.) is one of the most widely cultivated cereal crops in the world and serves as a staple food for millions of people across diverse agroecological regions. Alongside rice and wheat, maize contributes substantially to global food security, providing a major source of carbohydrates, protein, energy, vitamin B, and essential minerals (Iken, Amusa & Obatolu, 2002). Due to its adaptability to a wide range of climatic conditions and production systems, maize is cultivated on every continent except Antarctica. It plays a critical role in both subsistence and commercial agriculture.

Globally, maize production has increased significantly over the past decades due to advances in crop breeding, improved agronomic practices, and growing demand from food, feed, and biofuel industries (Series of Crop, n.d.; Ismail et al., 2016). However, despite these advances, maize production continues to face significant challenges arising from climate change, environmental degradation, emerging pests and diseases, and increasing pressure on natural resources. These challenges are particularly pronounced in developing regions where agriculture remains highly dependent on rainfall and where farmers have limited access to improved technologies and agricultural inputs.

In Sub-Saharan Africa (SSA), maize is the most important cereal crop and constitutes a major component of household diets. The crop contributes significantly to food security, as Nigeria produces about 43% of the maize grown in West Africa (Smith et al., 1997; Phillip, 2001; Iken & Amusa, 2004; McCann, 2005). According to (OECD/FAO, 2019), global maize production averages 1,127 million tons annually, with North America, Asia, and Africa being key producers. Due to its relatively high yields compared to other cereals, maize is especially appealing to farmers in regions with limited land and high population density (Shiferaw et al., 2011). Globally, 61% of maize production is allocated for livestock feed, while only 13% is consumed directly by humans: . As a result, any decline in maize productivity can have serious implications for food availability, nutrition, and economic well-being. Maize is expected to increase further as population growth and urbanization drive greater demand for affordable staple foods.

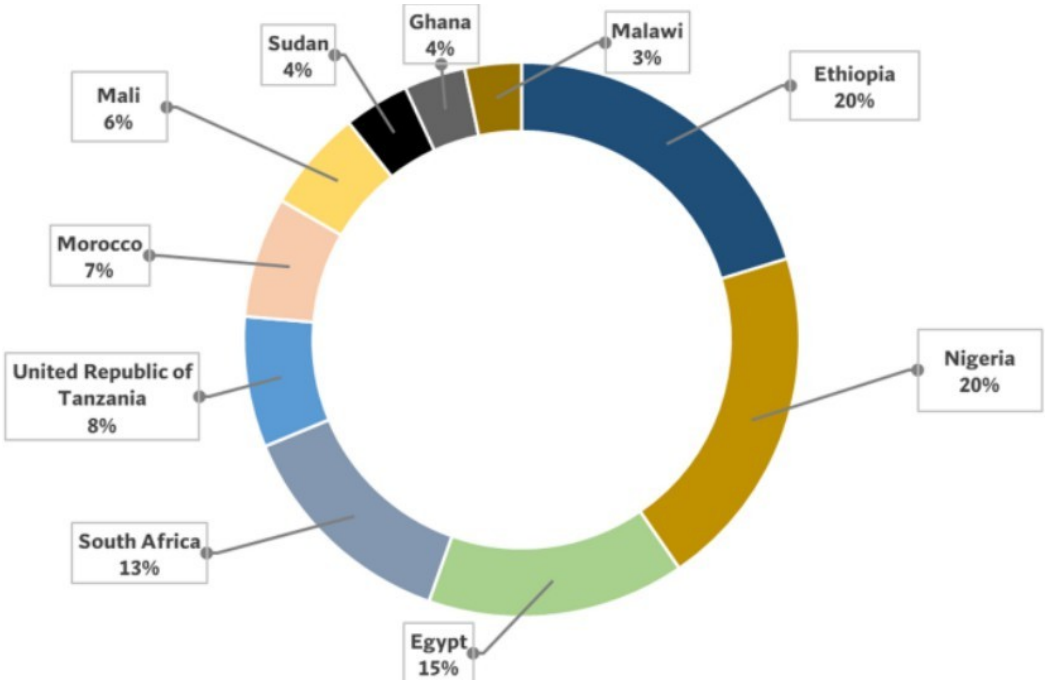


Figure 1. Top 10 producing countries of total cereal in Africa as of 2021. Percentage values are derived from total by the ten countries (cereal production not total production in Africa). Data obtained from: FAOSTAT

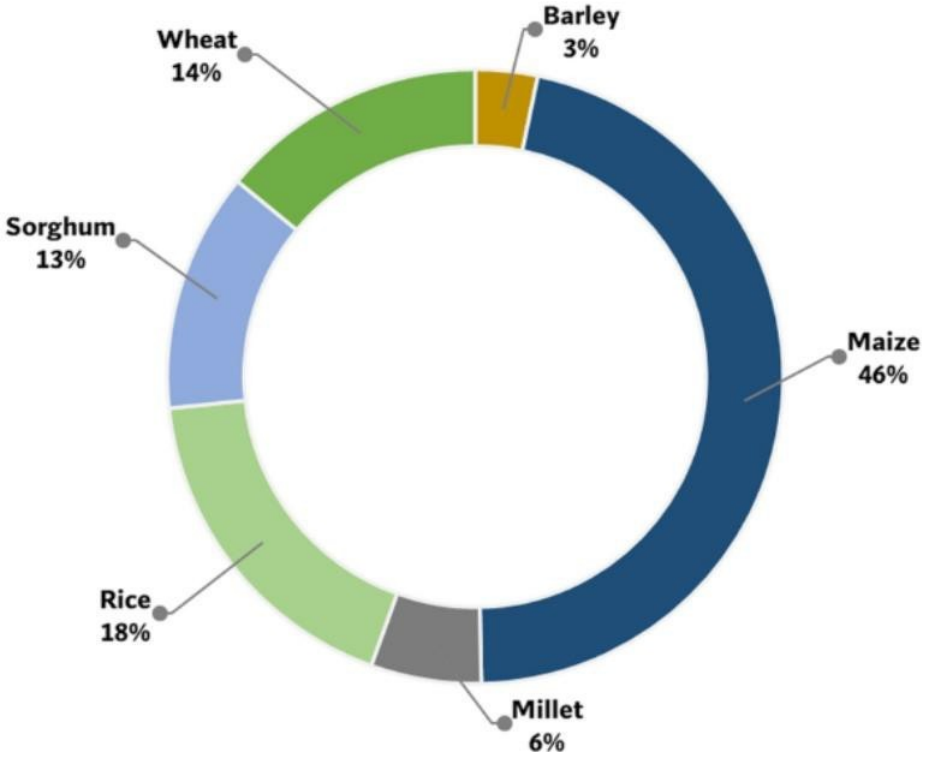


Figure 2. Percentage production of different cereal crops in Africa as of 2021. Maize is the most cultivated cereal followed by rice and wheat. Data obtained from: FAOSTAT

Nigeria is the largest producer of maize in West Africa and one of the leading producers on the African continent. The crop is cultivated across diverse agroecological zones and serves multiple purposes, including human consumption, livestock feed, and industrial processing. In

recent years, maize production has become increasingly important for supporting national food security and agricultural development initiatives. Nevertheless, maize productivity in Nigeria remains below its potential due to several constraints, including recurrent drought stress, declining soil fertility, limited access to improved seed varieties, and inadequate adoption of agricultural innovations. Nigeria has experienced remarkable growth in maize production over the last six decades, as evidenced by data from FAOSTAT (2022) and presented in Figure 3. In recent years, the country's annual maize production has consistently surpassed 10 million metric tons, establishing Nigeria as one of Africa's top maize-producing nations. With production levels reaching 12 million metric tons, Nigeria has solidified its position as the second-largest maize producer in Africa and the leading producer in West Africa. Between 2015 and 2020, the country accounted for more than 48% of the region's total maize output.

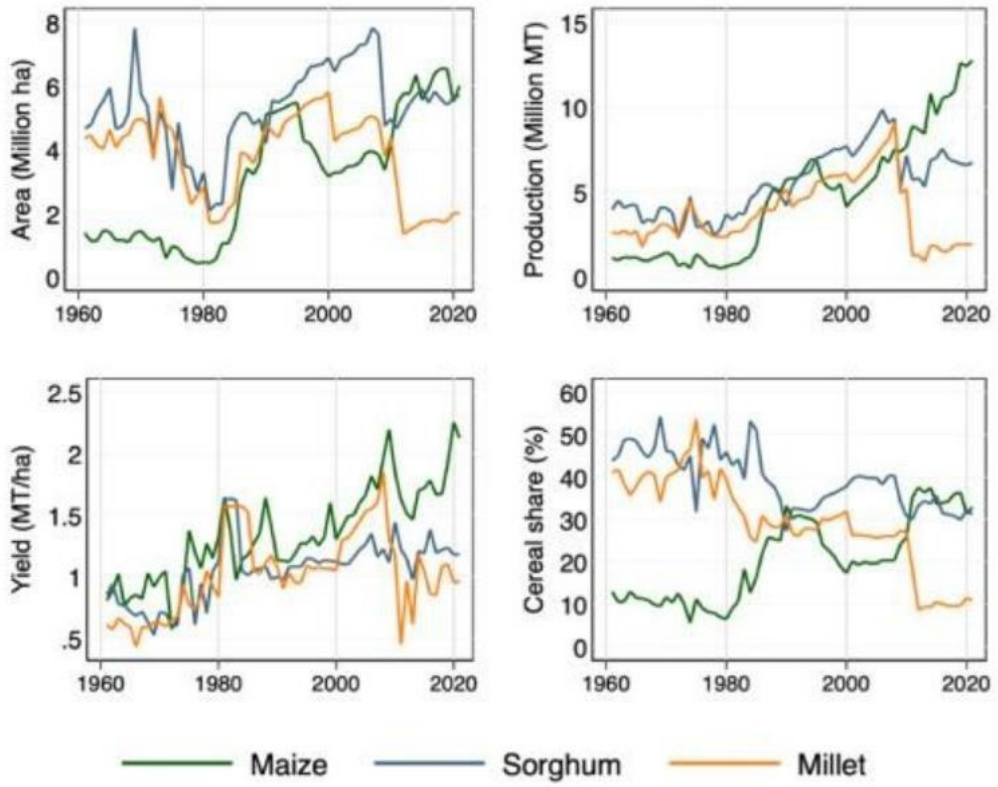


Figure. 3. Production, area and yield trends of maize, millet, and sorghum. Data obtained from: FAOSTAT

Given the central role of maize in food systems and rural livelihoods, improving the productivity, nutritional quality, and resilience of maize varieties has become a major priority for researchers, breeders, policymakers, and development organizations. Understanding how social, physiological, and genetic factors influence maize performance and adoption is therefore essential for developing varieties that meet both farmer needs and broader food security objectives.

1.2 Climate Change, Drought Stress and Maize Production

Climate change has emerged as one of the most significant threats to global agricultural productivity, particularly in regions where farming systems are heavily dependent on rainfall. Rising temperatures, changing precipitation patterns, and increased frequency of extreme weather events are expected to adversely affect crop production and food security worldwide (IPCC, 2023). Among the major cereal crops, maize is considered particularly vulnerable to

water deficits because of its relatively high-water requirement and sensitivity to drought during key developmental stages such as flowering and grain filling (Lobell et al., 2014).

Drought stress is widely recognized as one of the most important abiotic factors limiting maize productivity globally. It has been estimated that drought can reduce maize yields by 15–40%, depending on the severity, timing, and duration of the stress event (Farooq et al., 2017). The impact of drought is especially pronounced in Sub-Saharan Africa (SSA), where most maize production is undertaken by smallholder farmers under rain-fed conditions and where access to irrigation infrastructure remains limited (Cairns et al., 2013). The challenges posed by drought are of particular concern in Nigeria, where maize has become an increasingly important staple crop for both human consumption and livestock production. Although maize cultivation has expanded considerably in recent decades, productivity remains below global averages, partly due to environmental stresses including erratic rainfall and prolonged dry spells (FAO, 2023). Climate projections suggest that many maize-growing regions in West Africa will experience increased rainfall variability and more frequent drought events, potentially exacerbating existing production constraints (Sultan and Gaetani, 2016).

At the plant level, drought stress disrupts several physiological processes that are essential for growth and yield formation. Water limitation typically induces stomatal closure, reducing carbon dioxide uptake, and consequently decreasing photosynthetic activity (Flexas et al., 2004). Prolonged drought can also affect chlorophyll content, nutrient uptake, biomass accumulation, and reproductive development, ultimately resulting in reduced grain yield (Barnabás et al., 2008). Physiological traits such as stomatal conductance and photosystem II efficiency are therefore frequently used as indicators of drought tolerance because they provide insights into the ability of plants to maintain photosynthetic performance under water-limited conditions.
Importantly, substantial genetic variation exists among maize genotypes in their responses to drought stress. Previous studies have demonstrated that some genotypes can maintain physiological activity and productivity under drought conditions through mechanisms such as improved water-use efficiency, deeper rooting systems, osmotic adjustment, and enhanced antioxidant activity (Campos et al., 2004; Cairns et al., 2013). Understanding this variation is fundamental for breeding programs seeking to develop climate-resilient maize varieties capable of sustaining productivity under increasingly variable environmental conditions.

While considerable progress has been made in breeding maize for drought tolerance, the success of improved varieties ultimately depends on their acceptance by farming communities. Consequently, efforts to enhance drought resilience must be considered alongside farmer preferences and nutritional quality objectives. Integrating these dimensions is increasingly recognized as essential for developing maize varieties that are not only biologically superior but also socially acceptable and widely adopted.

1.3 Nutritional Quality, Hidden Hunger and Biofortification

Despite substantial improvements in global food production, malnutrition remains a major challenge in many developing countries. While considerable attention has traditionally focused on calorie deficiency, increasing recognition has been given to the problem of micronutrient deficiency, commonly referred to as "hidden hunger." Hidden hunger occurs when diets provide sufficient energy but lack adequate quantities of essential micronutrients required for normal growth, development, and physiological functioning (Bouis and Welch, 2010). Globally, more than two billion people are estimated to suffer from deficiencies of key micronutrients such as vitamin A, iron, and zinc (World Health Organisation, 2023). The

burden of micronutrient malnutrition is particularly severe in Sub-Saharan Africa, where diets are often dominated by starchy staple crops that provide energy but relatively low concentrations of essential vitamins and minerals (Bouis et al., 2011). The consequences of micronutrient deficiencies include impaired immune function, reduced cognitive development, increased susceptibility to disease, and adverse maternal and child health outcomes.

Maize plays a central role in food systems across Sub-Saharan Africa and serves as a major source of dietary energy for millions of households. In Nigeria, maize consumption has increased considerably over recent decades due to population growth, urbanization, and changing dietary preferences (IITA, 2022). Although maize contributes significantly to food security, conventional maize varieties are generally characterised by relatively low concentrations of provitamin A, iron, zinc, and certain essential amino acids. Consequently, populations that rely heavily on maize-based diets may remain vulnerable to micronutrient deficiencies despite adequate caloric intake (Pixley et al., 2013). Biofortification has emerged as a promising and sustainable strategy for addressing micronutrient deficiencies through agriculture. Biofortification involves the development of crop varieties with enhanced nutritional value through conventional breeding, agronomic approaches, or modern biotechnological techniques (Bouis and Saltzman, 2017). Unlike supplementation and industrial food fortification programs, biofortification seeks to improve the nutritional quality of crops before they reach consumers, thereby providing a long-term and potentially cost-effective intervention for resource-poor populations. Significant progress has been made in the development of biofortified maize varieties, particularly those enriched with provitamin A. Provitamin A maize has received considerable attention because vitamin A deficiency remains a major public health concern in many African countries. Studies have demonstrated that regular consumption of provitamin A maize can contribute to improved vitamin A intake and nutritional status among vulnerable populations (Saltzman et al., 2013). Similarly, breeding efforts have focused on improving protein quality and increasing concentrations of other essential micronutrients in maize grain. However, the success of biofortified crops depends not only on their nutritional characteristics but also on their acceptance by farmers and consumers.

Previous studies have reported that grain color, taste, cooking quality, yield potential, storage characteristics, and market demand can strongly influence variety adoption decisions (Fisher et al., 2019). In several African countries, white maize is often preferred for cultural, culinary, and market reasons, whereas biofortified provitamin A maize typically exhibits yellow grain color. These preferences may create challenges for the widespread adoption of nutritionally enhanced varieties despite their potential health benefits. The relationship between nutritional quality and farmer preference therefore represents an important but often overlooked dimension of crop improvement. Breeding programs have historically focused on increasing yield and stress tolerance, while nutritional objectives have frequently been treated as secondary considerations. Yet achieving sustainable improvements in food and nutrition security requires the development of varieties that simultaneously meet agronomic, nutritional, and socio-cultural needs. Understanding how farmers evaluate and prioritise different maize traits is therefore essential for designing breeding strategies that encourage adoption while addressing nutritional challenges. Given the increasing emphasis on nutrition-sensitive agriculture, there is a growing need to integrate nutritional quality considerations with farmer preferences and environmental resilience. Such an approach is particularly relevant in regions such as Kwara State, Nigeria, where maize plays a critical role in both livelihoods and household nutrition. Examining the interactions among these factors can provide valuable insights for the development of maize varieties that are both nutritionally beneficial and acceptable to farming communities.

1.4 Farmer Preferences, Variety Adoption and the Breeding–Adoption Gap

Farmer variety selection is a complex process influenced by agronomic, economic, social, cultural, and institutional factors. While breeders frequently prioritise traits such as yield, drought tolerance, and nutritional quality, farmers often evaluate varieties using a broader range of criteria, including grain colour, taste, maturity period, storage characteristics, market demand, seed availability, household consumption needs, and perceived production risks (Asrat et al., 2010; Weltzien et al., 2019). Consequently, the traits targeted by breeding programmes do not always align with those most valued by farming households.

Research conducted across Nigeria and other parts of Sub-Saharan Africa demonstrates that farmer decisions regarding maize cultivation are influenced not only by varietal characteristics but also by wider socio-economic and institutional factors. Access to extension services, participation in government and non-government agricultural programmes, seed availability, production resources, food security concerns, indigenous knowledge systems, and perceptions of biodiversity management have all been shown to influence adoption decisions and crop management strategies (Langyintuo et al., 2010; Fisher et al., 2015; Abate et al., 2017). Farmers frequently balance productivity objectives against household food security needs, resource constraints, market opportunities, and risk management considerations. The survey component of this study was designed to capture these multiple dimensions of farmer decision-making. Survey domains included maize varietal preferences, perceptions of nutritional quality, food security beliefs, participation in agricultural support programmes, farming practices, perceived barriers to crop diversification, resource constraints, and intended improvements to maize production systems. These variables were included because previous studies suggest that adoption of improved crop varieties is rarely determined by a single factor but instead emerges from interactions among farmer perceptions, available resources, social influences, and institutional support systems. Questions included in the survey were informed by previous studies examining farmer preferences, agricultural technology adoption, seed systems, biodiversity conservation, and biofortified crop adoption within Sub-Saharan Africa. The survey therefore sought to capture the range of factors previously identified as influencing farmer decision-making while generating context-specific evidence from maize-growing communities in Kwara State, Nigeria.

1.5 Breeding Maize for Drought Tolerance: Physiological and Genetic Perspectives

The increasing frequency and severity of drought events associated with climate change have intensified efforts to develop maize varieties capable of maintaining productivity under water-limited conditions. Improving drought tolerance has therefore become a major objective of maize breeding programs worldwide, particularly in regions such as Sub-Saharan Africa where agricultural production depends largely on rainfall and where drought remains a significant constraint to crop productivity (Cairns et al., 2013). Breeding for drought tolerance is inherently challenging because drought response is a complex trait controlled by multiple physiological, biochemical, and genetic mechanisms. Unlike traits governed by a small number of genes, drought tolerance results from the interaction of numerous processes that influence plant growth, water use, photosynthesis, and reproductive development.

Furthermore, the effects of drought vary depending on its timing, duration, intensity, and the developmental stage at which stress occurs (Bänziger et al., 2000). Maize is particularly sensitive to drought during flowering and grain-filling stages, when water deficits can

substantially reduce pollination success, kernel development, and final grain yield (Bolaños and Edmeades, 1996). As a result, research characterized to identify physiological traits that can serve as indicators of drought tolerance and facilitate the selection of superior genotypes. Such traits provide valuable insights into plant responses before yield losses become apparent and can improve the efficiency of breeding programs. Among the physiological traits commonly associated with drought tolerance, stomatal conductance has received considerable attention. Stomata regulate gas exchange between the plant and the atmosphere, controlling both carbon dioxide uptake for photosynthesis and water loss through transpiration. Under drought conditions, stomatal closure reduces water loss but also limits carbon assimilation, potentially reducing growth and productivity (Flexas et al., 2004). Genotypes that maintain an optimal balance between water conservation and photosynthetic activity may therefore exhibit improved drought tolerance. Photosystem II (PSII) efficiency is another important physiological indicator of plant stress responses. Photosystem II is a critical component of the photosynthetic apparatus responsible for capturing light energy and initiating electron transport during photosynthesis. Drought stress can impair PSII function through damage to photosynthetic machinery and reduced photochemical efficiency, leading to declines in plant performance (Baker and Rosenqvist, 2004). Measurements of PSII efficiency are therefore widely used to assess plant responses to environmental stress and to identify genotypes capable of maintaining photosynthetic function under adverse conditions.

In addition to physiological variation, substantial genetic diversity exists among maize varieties in their responses to drought stress. Genetic variation provides the foundation upon which plant breeding programs operate and enables the development of improved varieties with enhanced resilience. Previous studies have demonstrated considerable differences among maize genotypes in traits related to water-use efficiency, root architecture, osmotic adjustment, photosynthetic capacity, and stress recovery (Campos et al., 2004; Cairns et al., 2013). Understanding this variation is essential for identifying germplasm with desirable drought-tolerance characteristics and for informing future breeding efforts. Recent advances in plant breeding have increasingly emphasised the integration of physiological and genetic information to improve drought tolerance. Rather than relying solely on yield-based selection, researchers now recognize the importance of understanding the physiological mechanisms that contribute to stress adaptation and the genetic factors underlying these responses. Such approaches can facilitate the identification of maize varieties that not only survive drought conditions but also maintain acceptable levels of productivity and grain quality.

An additional consideration is the potential impact of drought stress on grain nutritional quality. While breeding programs have traditionally focused on maintaining yield under drought conditions, increasing attention is being given to how environmental stress affects nutritional traits. Drought can influence grain composition through its effects on plant metabolism, nutrient uptake, and resource allocation, potentially altering concentrations of proteins, carbohydrates, and other nutritionally important compounds (Prasanna et al., 2021). Consequently, understanding the relationship between drought tolerance and nutritional quality represents an important area of research for developing climate-resilient and nutrition-sensitive maize varieties. Despite significant advances in drought-tolerance breeding, important knowledge gaps remain regarding how physiological responses, genetic variation, and nutritional quality interact under drought conditions. Addressing these gaps is particularly relevant for regions such as Nigeria, where climate change, food security concerns, and nutritional challenges intersect. Investigating variation in drought responses among maize varieties can therefore provide valuable information for breeding programmes seeking to improve both resilience and nutritional outcomes.

1.6 Why Nigeria and Kwara State Matter

Nigeria is the largest producer of maize in West Africa and one of the leading producers on the African continent. Over the past three decades, maize production has expanded considerably due to increasing demand for human consumption, livestock feed, and industrial processing (FAOSTAT, 2023). The crop is cultivated across a wide range of agroecological zones and plays an important role in national food security, rural livelihoods, and economic development. Despite this importance, average maize yields in Nigeria remain substantially below their potential, reflecting persistent challenges associated with climate variability, declining soil fertility, pest pressures, limited access to improved seed, and constraints in agricultural extension services (Abate et al., 2017). As in many parts of Sub-Saharan Africa, maize production in Nigeria is dominated by smallholder farmers who often operate under rain-fed conditions and have limited capacity to buffer against environmental shocks. Consequently, changes in rainfall patterns and increasing drought frequency represent significant threats to both productivity and household food security. These challenges have intensified interest in the development of maize varieties that combine improved drought tolerance with desirable agronomic and nutritional characteristics.

Beyond production challenges, Nigeria continues to face substantial nutritional concerns. Micronutrient deficiencies remain prevalent among vulnerable populations, particularly women and children, despite ongoing efforts to improve food and nutrition security (HarvestPlus, 2022). Given the importance of maize in household diets, biofortified maize has been promoted as a potentially sustainable strategy for improving micronutrient intake. However, the success of such interventions depends not only on the nutritional superiority of improved varieties but also on their acceptance by farmers and consumers. Kwara State provides a particularly relevant context for examining these issues. Located within Nigeria's Guinea Savannah zone, the state is characterised by favourable conditions for maize cultivation and agriculture remains a major source of livelihood for much of the rural population. Maize is widely grown across the state for both household consumption and commercial purposes, making it an important component of local farming systems. However, farmers in the region face many of the same challenges observed elsewhere in Nigeria, including variable rainfall, increasing production costs, limited access to improved technologies, and fluctuating market conditions.

Importantly, relatively few studies have attempted to integrate social, physiological, and genetic perspectives when examining maize production within Kwara State. Existing research has often focused on either agronomic performance, nutritional quality, or farmer behaviour in isolation. While such studies have generated valuable insights, they provide only a partial understanding of the factors influencing maize production and adoption decisions. There remains limited evidence regarding how farmer preferences align with nutritional objectives, how drought stress influences nutritionally important traits, and how genetic variation contributes to differences in drought response among maize varieties relevant to the region. The present study addresses these gaps by adopting a multidisciplinary approach that examines maize trait variation across social, physiological, and genetic scales. By integrating farmer perspectives with physiological and genetic assessments, the study seeks to generate evidence that can inform the development and promotion of maize varieties that are not only resilient to environmental stress but also responsive to local needs and preferences. Such information is particularly valuable for supporting future breeding programs and agricultural development initiatives in Kwara State and comparable maize-growing regions of Nigeria.

1.7 Theoretical and Conceptual Framework

To understand the factors influencing maize variety selection and adoption, this study draws upon the Theory of Planned Behaviour (TPB) (Ajzen, 1991). The Theory of Planned Behaviour has been widely applied in agricultural technology adoption research and provides a robust framework for explaining how attitudes, social influences, and perceived constraints shape farmer decision-making (Fielding et al., 2008; Rezaei et al., 2019).

According to TPB, behaviour is influenced by behavioural intentions, which are themselves determined by three key constructs: attitudes toward a behaviour, subjective norms, and perceived behavioural control. Within the context of maize production, attitudes reflect farmers' evaluations of maize varieties and their characteristics, including yield potential, nutritional quality, drought tolerance, grain colour, marketability, and food-use value. Subjective norms refer to social influences arising from extension services, community leaders, neighbouring farmers, family members, agricultural programmes, and local markets. Perceived behavioural control reflects the extent to which farmers believe they possess the resources and opportunities required to adopt a particular variety, including access to seed, land, labour, technical knowledge, financial resources, and institutional support. The survey variables used in this study were selected to reflect these behavioural dimensions. Measures relating to maize preferences, nutritional perceptions, food security beliefs, and intended production improvements correspond to attitudinal components of the model. Participation in government and non-government agricultural programmes, information sources, and social learning opportunities reflect subjective norms. Variables relating to seed access, resource limitations, production constraints, indigenous farming practices, and barriers to increasing crop biodiversity reflect perceived behavioural control.
The inclusion of these factors is particularly important because farmer adoption of nutritionally enhanced or drought-tolerant maize varieties depends not only on the biological superiority of the varieties themselves but also on whether farmers perceive them as beneficial, socially acceptable, and practically achievable within their local production systems. Consequently, the Theory of Planned Behaviour provides a useful framework for interpreting the relationships among farmer preferences, nutritional quality, and adoption decisions examined in this study

The social component of this study utilised a limited number of Likert-scale items to assess farmer perceptions. Although longer scales are often recommended for measuring complex psychological constructs, shorter scales are frequently used in agricultural surveys conducted in rural settings where literacy levels, interview duration, respondent burden, and field logistics must be carefully balanced. In the present study, the Likert-scale items were intended to provide indicative measures of farmer attitudes rather than comprehensive psychometric assessments of behavioural constructs. Consequently, findings derived from these items are interpreted alongside descriptive and qualitative survey responses rather than standalone psychological measures.
The Theory of Planned Behaviour also provides a framework for interpreting the study findings within the Discussion chapter. Specifically, the extent to which farmer preferences, social influences, and practical constraints explain varietal choice and adoption behaviour is evaluated in relation to TPB predictions, allowing the study to contribute not only empirical findings but also theoretical insight into agricultural decision-making within smallholder maize systems.

1.8 Knowledge Gaps and Rationale for the Study

Considerable progress has been made in understanding the agronomic, physiological, and nutritional aspects of maize production. Similarly, a growing body of research has examined farmer preferences and the adoption of improved maize varieties across Sub-Saharan Africa. However, despite these advances, important gaps remain in the literature that limit the development of integrated maize improvement strategies capable of addressing the interconnected challenges of food security, nutrition, and climate resilience.

First, while numerous studies have investigated farmer preferences for maize varieties, much of the existing research has focused primarily on agronomic traits such as yield, maturity period, pest resistance, and grain characteristics (Weltzien et al., 2019). Comparatively less attention has been given to understanding how farmers perceive nutritional quality traits and how these traits influence variety selection decisions. Furthermore, studies have often examined farmer preferences independently of broader breeding objectives, resulting in limited understanding of how farmer priorities align with efforts to promote nutritionally enhanced or climate-resilient maize varieties.
Second, although biofortification has emerged as a promising strategy for addressing micronutrient deficiencies, evidence suggests that nutritional improvements alone do not guarantee adoption by farmers or acceptance by consumers (Bouis and Saltzman, 2017). In many African contexts, grain colour, taste, processing characteristics, and market preferences continue to influence variety selection decisions. However, relatively few studies have examined the potential trade-offs between nutritional quality objectives and farmer preferences within the Nigerian context. This represents an important knowledge gap because successful biofortification programmes ultimately depend on both nutritional effectiveness and user acceptance. Third, substantial research has been conducted on drought tolerance in maize, particularly with respect to physiological responses and genetic variation under water-limited conditions (Cairns et al., 2013). Nevertheless, much of this work has focused on yield-related outcomes, while comparatively less attention has been given to understanding how drought stress influences nutritional quality traits. As climate change continues to increase drought risk in many maize-growing regions, there is a growing need to understand whether improvements in drought tolerance can be achieved without compromising grain nutritional quality.

A further limitation of the existing literature is that social, physiological, and genetic dimensions of maize improvement are often investigated separately. Studies examining farmer behaviour typically focus on socio-economic factors influencing adoption, whereas physiological and genetic studies primarily investigate plant responses to environmental stress. Although these approaches have generated valuable knowledge, they provide only a partial understanding of the factors influencing the success of improved maize varieties. There remains limited evidence regarding how farmer preferences, nutritional quality, drought tolerance, and genetic variation interact to influence the development and adoption of maize varieties suitable for smallholder farming systems. These gaps are particularly relevant in Nigeria, where maize plays a critical role in both food security and rural livelihoods. Despite the importance of maize production in Kwara State, relatively little research has integrated social, physiological, and genetic perspectives to examine trait variation and its implications for variety improvement and adoption. Addressing this gap is important because breeding programmes increasingly face the challenge of developing varieties that satisfy multiple objectives simultaneously, including productivity, nutritional quality, environmental resilience, and farmer acceptability.

The present study was therefore designed to address these knowledge gaps by adopting a

multidisciplinary approach that investigates maize trait variation across social, physiological, and genetic scales. By examining farmer preferences, nutritional quality, drought stress responses, and genetic variation within a single research framework, the study seeks to contribute a more comprehensive understanding of the factors influencing maize improvement and adoption in Kwara State, Nigeria.

1.9 Aim and Objectives of the Study

1.9.1 Overall Aim

The overall aim of this study was to investigate trait variation in maize across social, physiological, and genetic scales, and to evaluate how these variations influence farmer preferences, nutritional quality, and drought stress responses in maize varieties cultivated in Kwara State, Nigeria.

1.9.2 Research Objectives

To achieve this aim, the study pursued the following objectives:

1. To identify the key traits influencing smallholder farmer preferences for maize type and nutritional quality in Kwara State, Nigeria.
2. To evaluate the nutritional quality of commonly cultivated maize varieties in Ilorin, Kwara State.
3. To assess the impact of drought stress on key nutritional components of selected maize varieties.
4. To explore genetic variation in drought stress responses and its relationship with maize nutritional quality.

1.10 Research Questions

The study was guided by the following research questions:

1. Which maize traits most strongly influence smallholder farmer preferences and variety selection in Kwara State, Nigeria?
2. What are the nutritional characteristics of commonly cultivated maize varieties in Ilorin, Kwara State?
3. How does drought stress affect key nutritional components of selected maize varieties?
4. To what extent do maize varieties differ in their physiological and genetic responses to drought stress?
5. How can information on farmer preferences, nutritional quality, and drought tolerance be
   integrated to support the development and adoption of improved maize varieties in Nigeria?

1.11 Significance of the Study

This study contributes to the growing body of literature on maize improvement by adopting an integrated approach that examines trait variation across social, physiological, and genetic scales. While previous studies have frequently investigated farmer preferences, nutritional quality, and drought tolerance separately, relatively few have attempted to understand how these factors interact to influence the development and adoption of improved maize varieties. By bringing these dimensions together within a single research framework, the study provides a more comprehensive understanding of the challenges and opportunities associated with maize

improvement in Nigeria.

From a social perspective, the study contributes to knowledge on farmer decision-making and variety selection. Understanding the traits valued by smallholder farmers is essential for ensuring that breeding programmes develop varieties that are not only technically superior but also relevant to the needs and preferences of intended users. Insights from the study may therefore support more demand-driven and farmer-centred breeding strategies. From a nutritional perspective, the study provides information on variation in the nutritional quality of maize varieties cultivated within the study area. Such information is important in the context of ongoing efforts to address micronutrient deficiencies and improve dietary quality through agricultural interventions. The findings may contribute to discussions surrounding biofortification and the promotion of nutritionally enhanced crop varieties in Nigeria. From a physiological and genetic perspective, the study advances understanding of how maize varieties respond to drought stress and how genetic variation influences these responses. Given increasing concerns regarding climate change and rainfall variability, identifying traits associated with drought tolerance remains an important priority for maize improvement programmes. The findings may therefore contribute to future efforts aimed at developing climate-resilient maize varieties capable of maintaining performance under water-limited conditions.

The study also has practical relevance for plant breeders, agricultural extension practitioners, policymakers, and development organisations. By highlighting the relationships among farmer preferences, nutritional quality, and drought tolerance, the findings may support the design of maize improvement programmes that better align breeding objectives with the realities of smallholder farming systems. Ultimately, the study seeks to contribute towards the development of maize varieties that can simultaneously enhance food security, improve nutritional outcomes, and strengthen resilience to climate-related stresses. More broadly, the study responds to the growing recognition that agricultural challenges cannot be adequately addressed through disciplinary approaches alone. By integrating social and biological perspectives, the research provides evidence that may inform more holistic and sustainable approaches to crop improvement in Nigeria and other maize-producing regions of Sub-Saharan Africa.

1.12 Thesis Structure

This thesis is organized into four chapters.

Chapter One provides a general introduction to the study. It reviews the importance of maize in global and Sub-Saharan African food systems, examines the challenges posed by climate change and drought stress, discusses issues relating to nutritional quality and biofortification, and explores the role of farmer preferences in maize variety adoption. The chapter also presents the theoretical and conceptual framework, identifies key knowledge gaps, and outlines the aims, objectives, and research questions that guided the study.

Chapter Two, entitled *Impact of Smallholder Farmer Preferences on Maize Nutritional Quality*, investigates the factors influencing maize variety selection among smallholder farmers in Kwara State, Nigeria. The chapter examines farmers' preferences for different maize traits, evaluates perceptions relating to nutritional quality, and explores how these preferences may influence the adoption of nutritionally enhanced maize varieties. The findings provide insights into the social dimensions of maize improvement and contribute to understanding the relationship between farmer preferences and breeding objectives.

Chapter Three, entitled *Studies on Genetic Variation for Drought Tolerance and Water Use*

Efficiency in Maize, examines the physiological and genetic responses of selected maize varieties to drought stress. The chapter evaluates variation in drought-related traits associated with water-use efficiency and plant performance under water-limited conditions. It further investigates the effects of drought stress on nutritional quality and explores genetic variation among maize varieties in their responses to environmental stress. The findings contribute to understanding the mechanisms underlying drought tolerance and their implications for maize improvement under changing climatic conditions.

Chapter Four presents the general discussion and conclusions of the thesis. The chapter integrates findings from the social, physiological, and genetic components of the study and evaluates their implications for maize breeding, nutritional improvement, drought resilience, and variety adoption. The chapter discusses how farmer preferences, nutritional quality, and drought tolerance can be considered simultaneously within maize improvement programs. The chapter also highlights the main contributions of the research, acknowledges study limitations, and provides recommendations for future research, policy, and breeding initiatives.

2.0 Chapter two: The impact of farmer preferences on maize nutritional quality: A focus on smallholder farmers in Sub-Saharan Africa

2.1 Introduction

Maize is a major staple crop for millions of households across Sub-Saharan Africa and plays a central role in food security, income generation, and rural livelihoods. In Nigeria, maize is cultivated extensively by smallholder farmers under predominantly rain-fed conditions and contributes substantially to both household consumption and local markets (Onumah et al., 2021; FAOSTAT, 2022). Despite its importance, the success of maize improvement programmes depends not only on agronomic performance but also on the extent to which improved varieties meet the needs and preferences of farmers who ultimately decide which varieties are cultivated and maintained within local production systems. Farmer preferences are increasingly recognised as an important component of crop improvement and agricultural development. Although plant breeders often prioritise traits such as yield potential, drought tolerance, disease resistance, and nutritional quality, farmers frequently evaluate varieties using a broader set of criteria that reflect their production realities and livelihood objectives. These criteria may include grain colour, taste, market demand, maturity period, storage characteristics, seed availability, and adaptation to local environmental conditions (Asrat et al., 2010; Sibiya et al., 2013; Marenya et al., 2021). Consequently, varieties that perform well in experimental trials may not achieve widespread adoption if they fail to align with farmer priorities. Understanding farmer preferences has become particularly important in the context of nutrition-sensitive agriculture. While maize provides a substantial proportion of daily caloric intake in many African countries, concerns remain regarding the nutritional adequacy of maize-based diets, especially among households with limited access to diverse food sources (Nuss and Tanumihardjo, 2010). Efforts to improve the nutritional quality of maize through biofortification and breeding have generated varieties with enhanced concentrations of provitamin A and other nutritionally important compounds (Bouis and Saltzman, 2017; Prasanna et al., 2021). However, the success of these initiatives depends on whether farmers are willing to cultivate such varieties and whether consumers are willing to purchase and consume them.

Previous studies have shown that farmer preferences for maize varieties are influenced by a combination of agronomic, economic, cultural, and nutritional considerations. Across many parts of Africa, white maize remains the preferred grain type because of its familiarity, culinary qualities, and strong market demand, whereas yellow maize has historically faced lower acceptance despite its potential nutritional advantages (De Groote et al., 2002; Stevens and Winter-Nelson, 2008; Ranum et al., 2014). However, recent biofortification initiatives and increasing awareness of nutritional benefits have contributed to changing perceptions of yellow maize in some regions (Meenakshi et al., 2012; De Groote et al., 2016). These trends suggest that varietal preferences are dynamic and may evolve in response to changing environmental conditions, market opportunities, and nutritional awareness. Smallholder farmers also play an important role as informal selectors within agricultural systems. Through their decisions regarding seed saving, seed exchange, variety choice, and crop management, farmers influence which varieties persist and which are gradually abandoned. These decisions are often shaped by experiences of environmental stress, particularly drought, which remains one of the most significant constraints to maize production in Sub-Saharan Africa. As a result, farmer perceptions of varietal performance under drought conditions can strongly influence adoption decisions and contribute to on-farm selection pressures that operate alongside formal breeding

programmes (Soleri and Cleveland, 2009).

In Nigeria, relatively limited research has examined how farmer preferences interact with maize nutritional quality at the local level. While studies have investigated maize production, varietal adoption, and nutritional improvement separately, fewer studies have attempted to connect farmer decision-making with measurable differences in nutritional quality among commonly cultivated maize types. Understanding this relationship is important because varieties that are nutritionally superior may not necessarily be those most widely cultivated, while farmer-preferred varieties may not always provide optimal nutritional benefits.

This chapter therefore investigates the impact of smallholder farmer preferences on maize nutritional quality in Ilorin South Local Government Area of Kwara State, Nigeria. Using questionnaire data collected from smallholder maize farmers alongside protein analysis of maize grain samples, the chapter examines varietal preferences, seed sourcing practices, perceptions of drought stress, and variation in grain protein content among commonly cultivated maize types. By linking farmer perspectives with nutritional measurements, the chapter provides insight into how social factors influence the cultivation of maize varieties and the nutritional outcomes associated with smallholder production systems.

2.2 Smallholder Farmer Preferences for Maize

Numerous studies have investigated farmer's preferences for crop variety attributes, examining various factors influencing their decisions. These studies have provided valuable insights into the diverse needs and priorities of farmers across different regions, emphasizing the importance of understanding local contexts and preferences when developing and promoting crop varieties. Farmer's priorities and preferences for maize variety traits can vary significantly between individuals and across different agro-ecological zones (Mansaray et al., 2019; Witcombe et al., 2005). Several factors, including farmer education, market accessibility, and socio-cultural attitudes towards modern agricultural practices, play a significant role in influencing seed selection decisions (Wulandari et al., 2024).

Yellow maize has experienced a surge in demand for use as animal feed due to its ability to impart a desirable deep yellow coloration to egg yolks, poultry skin, and animal fat (Anthony, 2014; Iken & Amusa, 2004). The increasing demand for yellow maize as animal feed may lead to a decline in its availability for human consumption in Africa. In a survey conducted by Pillay et al. (2011), several respondents expressed their perception that yellow maize is exclusively found in shops selling animal feed, suggesting it is only suitable for animal consumption. The preference for white maize in food production can be attributed to a combination of cultural, social, and historical factors. These include the belief that "white is superior" or "the whiter, the better," the influence of indigenous staple crops, government policies, organoleptic differences, a desire for visually appealing dishes, and familiarity with white maize as a traditional dietary component Khumalo et al., 2011, McCann, 2005, Muzhingi et al., 2008b, Pillay et al., 2011, Ranum et al., 2014; White and Johnson, 2003).

In Eastern Africa, yellow maize is not commonly available in Kenyan markets, and there is a notable preference for white maize among consumers. According to a study conducted by De Groote and Kimenju (2012), only 26% of the respondents expressed a willingness to purchase yellow maize at the same price as white maize. Despite the potential for higher yields with hybrid maize varieties, farmers in Malawi, Zambia, and Zimbabwe have been found to prefer growing local landraces due to their taste and other desirable traits (Lunduka et al., 2012; Sibiya

et al., 2013). Similarly, a study conducted by Hebinck et al. (2015) in Luoland, Kenya, revealed that farmers preferred the taste of local maize varieties over available hybrid maize

In Cameroon, farmer's preferences for maize varieties are largely oriented towards traits such as large grain size, soft grain texture, large ear size, high prolificacy, early maturity, short plants, resistance to lodging, resistance to diseases, and reduced post-harvest losses (Mafouasson et al., 2020). In South Africa, farmers have distinct preferences for maize variety traits, which include high yield and prolificacy, disease resistance, early maturity, white grain colour, and desirable drying and shelling qualities (Sibiya et al., 2013). In contrast, Asrat et al. (2010) conducted a study on farmers' preferences for cereal crop varieties in Ethiopia and found that the primary focus was on yield stability and adaptability to the environment. In Kenya, Marenya et al. (2021) determined that maize breeding programs should prioritize drought and striga tolerance, as well as traits related to grain characteristics that improve storage ability. According to Abera et al. (2020), the adoption of maize varieties is not solely dependent on variety-specific traits but is also influenced by various production and market-related factors. These include soil fertility, fertilizer cost, seed cost, and market appreciation. Kassie et al. (2017) analysed farmer's preferences and willingness to pay for drought-tolerant maize varieties in Zimbabwe using choice experimental data. Their study highlighted the significance of drought tolerance as a preferred trait among local farmers.

Smallholder farmer preferences for maize are complex and influenced by multiple factors, including yield potential, resistance to stressors, nutritional quality, market demand, cultural traditions, and access to improved seeds. Farmers' preferences and perceptions of improved crop varieties have been identified crucial factors impacting their adoption and continued utilization (Marenya et al., 2021). Smallholder farmers in Tanzania face significant challenges in accessing improved seeds, largely due to various socio-economic factors. These challenges include limited access to information, inadequate infrastructure, and financial constraints that impede their ability to adopt advanced agricultural techniques. Despite the potential benefits of utilizing certified maize seed varieties, such as improved resilience to climate variability and higher yields, a significant number of smallholder farmers in Tanzania still rely on traditional seed sources. This reliance often results in breeding programs, extension services, and seed distribution strategies lower production efficiency and reduced yields (Lyimo et al., 2014). To enhance the adoption of improved maize varieties that balance productivity with nutritional and environmental resilience, it is crucial to incorporate farmer priorities.

2.3 Nutritional Quality of Maize

The maize kernel is the edible and nutritious part of the plant, with its composition detailed in Table 1. Green maize consumption constitutes a considerable portion of overall maize intake in Africa. The preparation of fresh maize dishes involves harvesting the ears during the milky to doughy stage, typically occurring three to five weeks after silking. The maize is then cooked using methods such as boiling, steaming, or roasting and subsequently consumed alongside various accompaniments, including herbs, spices, condiments, and vegetables (Alamu et. al.,2015). When maize kernels are at the milky stage, they possess a high sugar content. However, it is important to note that the concentrations of other essential nutrients may be lower than those found in kernels harvested at maturity (Alamu et. al.,2014). In many major maize-producing countries, street vendors offer boiled and roasted maize in various locations, making it a popular snack for school children (Alamu et.al., 2015; Olayiwola et. al., 2016). During the harvest season, roasted and boiled maize is a daily staple for over 50% of the population in Nigeria (Olayiwola et. al., 2016). Similarly, in Zimbabwe, approximately 48% of the population consumes boiled or roasted maize at least once a day (Muzhingi et.al., 2008). It is rich in

essential vitamins, including vitamin C, vitamin E, vitamin K, and several B-complex vitamins such as B1 (thiamine), B2 (niacin), B3 (riboflavin), B5 (pantothenic acid), B6 (pyridoxine), and folic acid. Additionally, it contains selenium, N-p-coumaryl tryptamine, and N-ferrulyl tryptamine. Potassium is a key nutrient in maize, which is particularly beneficial as most human diets lack enough of it (Kumar & Jhariya, 2013). Roasted maize kernels can also be used as a coffee substitute (Breadley, 1992).

Freshly harvested maize is prepared through cooking or boiling in salted water until the kernels become tender. Boiling the maize with the husk is a common practice, as it signifies freshness and helps to preserve nutrients and flavour. Roasting is performed using hot charcoal over a wire gauze, beside a fire, or within hot ashes until the maize attains a brownish hue. Both methods involve consuming the maize directly on the cob, often accompanied by a variety of spices and vegetables. The process of roasting with charcoal imparts a distinct aroma and flavour to the kernels. Conversely, roasting maize with the husk is not typically done, as it negatively affects sensory attributes like aroma, chewiness, taste, and appearance (Alamu et.al., 2015). Although the specific preferences of African consumers for green whole cob and kernel maize have not been clearly defined, it appears that freshness is a critical attribute (De Groote et.al., 2012). The physical properties of maize are considerably influenced by both the time of harvest and the specific variety. Maize that is harvested at a very mature stage (27-34 days after pollination) is found to be unsuitable for preparing roasted or boiled green maize dishes (Alamu et.al., 2015). In general, there are several key attributes of green maize that are of particular interest to consumers and producers. These attributes include soft endosperm, which contributes to a pleasing texture; a soft or thin hull for ease of consumption; a sweet taste that appeals to consumer preferences; and resistance to bursting, popping, or burning during the roasting process (De Groote et.al., 2012; Alamu et.al., 2015; Dovlo , 1973; Iken, 2004). Green maize can also be canned to provide opportunity to make available all year round and reduce the chances of mycotoxin contamination, which is a common concern when maize is dried and stored on farms. This can contribute to improved food safety for consumers while also expanding market opportunities for farmers by allowing them to offer a value-added product with a longer shelf life and reduced risk of spoilage.

Nutritional component	g
Carbohydrate	71.88
Protein	8.84
Fat	4.57
Fiber	2.15
Ash	2.33
Moisture	10.23
Phosphorous	0.348
Sodium	0.02
Sulphur	0.01
Amino acids	$1x10^{-3}$
Minerals	1.5
Calcium	0.01
Iron	$2x10^{-3}$

Potassium	0.229
Thiamine	$4x10^{-4}$
Vitamin C	$4*10^{-4}$
Magnesium	0.139
Copper	$4*10^{-4}$

Table 1. Typical nutritional composition (per 100g) of edible portion of maize. Source: Shah, Prasad, and Kumar (2015); Gopalan, Rama Sastri, and Balasubramanian (2007).

In various regions of Africa, such as East, West, and Central Africa, whole dried maize grains are often prepared with alkaline rock salt, which goes by various names like kaun, akanwu, trona, or magadi, as well as white wood ash. This cooking method offers several benefits, including shorter cooking times, improved digestibility, increased soup viscosity, and enhanced flavor. Moreover, the alkaline substances used in this cooking process also serve as preservatives and tenderizers, resulting in more palatable and longer-lasting dishes (Uzogara et. al., 1990). The Akanwu cooking process in Africa, like the nixtamalization technique in Mexico, has not been extensively researched yet. Indeed, in Mexico, the nixtamalization process is widely used to produce over 300 different food products, including the well-known tortilla (Palacios-Rojas et.al., 2016). Additionally, this process enhances the flavour of maize, contributing to its popularity as a staple in Mexican cuisine. Nixtamalization, a traditional Mesoamerican process used in maize preparation, offers several nutritional benefits (Figure. 4), it include (1) it reduces the risk of pellagra, a disease caused by niacin deficiency (2) increased calcium content in maize kernels during the steeping process with calcium hydroxide (3) contributes to a higher dietary fibre content in maize-based food products, specifically by increasing the amount of resistant starch (4) its ability to significantly reduce mycotoxin levels in maize kernels, particularly through the removal of the pericarp and (5) plays a role in reducing phytic acid content in maize kernels, which is beneficial for human nutrition. Phytic acid is an anti-nutritional factor that can inhibit the absorption of essential minerals like iron and zinc in the human digestive system. (Serna-Saldivar et.al., 2016. Bressani et.al., 2002). The nixtamalization process has been reported to effectively reduce mycotoxin contamination in maize through a combination of extraction and hydrolysis (Voss et.al., 2017; Elias-Orozco et.al., 2002).

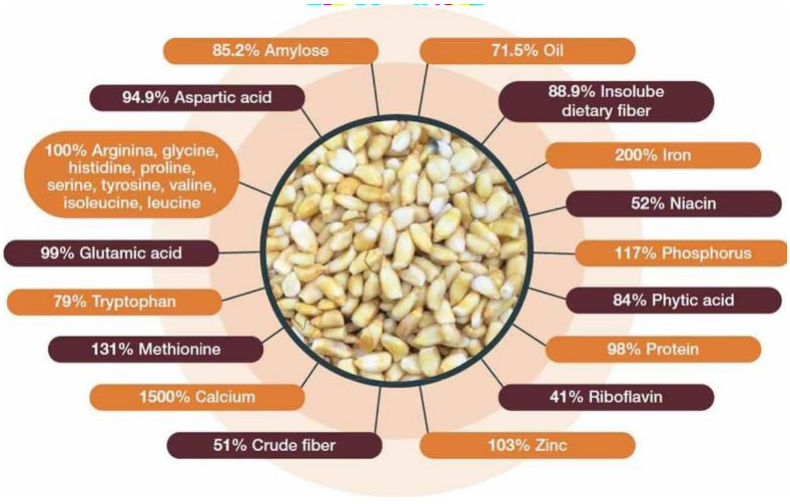


Figure 4. An overview of compound retention in nixtamalized maize. The increase in mineral composition along with a decrease in anti-nutrient as well as high retention of amino acid is beneficial to the fight against the rampant hidden hunger and protein-energy malnutrition (PEM) in Africa. Source: Onu Ekpa, Natalia Palacios-Rojas, Gideon Kruseman, Vincenzo Fogliano & Anita R. Linnemann, 2019

2.4 Breeding for Enhanced Nutritional Quality

Earlier research at the International Institute of Tropical Agriculture (IITA) identified genetic variation in carotenoid content among tropical maize inbred lines. However, the levels of provitamin A (PVA) carotenoids were low, leading to the incorporation of exotic germplasm to enhance carotenoid content (Menkir et al., 2015). To develop nutritionally enriched tropical maize varieties and hybrids, IITA collaborated with stakeholders from both the public and private sectors. A key initiative in this effort was the global HarvestPlus Challenge Program which made substantial investments in IITA and its partners to increase maize provitamin A content through conventional breeding. This collaboration resulted in the development and release of nutritionally enhanced maize hybrids, open-pollinated varieties, and elite parental inbred lines. Additionally, IITA partnered with CIMMYT (cimmyt.org) and other research institutions to exchange germplasm and molecular tools essential for improving maize nutrition. The IITA maize breeding program collaborates with various countries in the region to test nutritionally enhanced maize varieties. Alongside public research organizations, private seed companies play a vital role in testing and releasing these improved varieties. Over the years, biofortified maize has been distributed to farmers across multiple African nations through seed distribution programs, research collaborations, and partnerships with local agricultural institutions. These initiatives have increased the availability of nutrient-rich maize and encouraged its adoption among smallholder farmers. This approach leveraged novel genes from temperate and tropical maize germplasm, enabling the development of tropical-adapted maize varieties with high β-carotene and other carotenoid levels (>15 μg g−1) to enhance provitamin A content. As a result, numerous high-provitamin A varieties and hybrids (>15 μg g−1) were developed without compromising grain yield or other adaptive traits necessary for profitable maize cultivation in Africa (Menkir et al.,2021). Farmers have played a strategic role in this effort by participating in site-specific on-farm trials, where they compared their preferred maize varieties and hybrids with promising provitamin A-rich alternatives. This farmer-driven selection process has supported the registration, release, and commercialization of the best-performing varieties. Between 2012 and 2022, 18 varieties and 22 hybrids with intermediate to high provitamin A levels were released in Cameroon, the Democratic Republic of Congo, Burundi, Ethiopia, Ghana, Mali, Nigeria, and Zambia. In West Africa, over 34 open-pollinated varieties (OPVs) and hybrids developed by IITA and national program partners have been released. Several of the released maize varieties and hybrids achieve the HarvestPlus Challenge Program's breeding target of 15 μg g−1 provitamin A content. Between 2012 and 2023, a total of 76 vitamin A-fortified open-pollinated varieties (OPVs) and hybrids, adapted to various agroecological zones, were released across 11 African countries.

Between 2014 and 2021, a total of 27,337 tons of certified seeds of provitamin A-biofortified maize varieties were produced in Ghana, Mali, and Nigeria, supplying farmers who cultivated an estimated 1,093,464 hectares. This initiative benefited approximately 2,733,661 households in both rural and urban areas, based on an average household size of 10.3 in these countries. A national food consumption and nutrition survey conducted in Nigeria in 2021 and 2022 found that 13.4% of respondents had consumed provitamin A-biofortified orange maize or its derived products within the past 30 days. Consumption was particularly high in the Northeast region (38%), driven by government and donor-supported programs addressing food security challenges in the area (FGN; IITA, 2022). Additionally, the growing adoption of provitamin A-

biofortified maize has enhanced its market competitiveness by expanding its use in various food products and targeting niche markets. Notably, the number of biofortified maize varieties in Africa surpasses that of other biofortified crops.

2.5 Genomic-Enhanced Improvement

Extensive research on the genetics and genomics of plant carotenoid pathways (Sun et al., 2022) has significantly expanded our understanding, enabling the accelerated development of biofortified crops. The molecular and biochemical analysis of the carotenoid biosynthetic pathway has created new opportunities to enhance genetic improvements for carotenoid accumulation in maize (Sun et al., 2020; Hannoufa et al., 2012; Yuan et al., 2015). Advances in genomics and emerging disciplines have greatly facilitated rapid cultivar development. Three key pillars of genomic-led breeding include the availability of cost-effective, high-throughput genotyping methods, precise and scalable plant phenotyping technologies, and advanced data acquisition, storage, and analysis systems. Leveraging these technologies allows for an efficient assessment of genetic variability across a vast genetic pool, supporting the development of PVA-biofortified maize cultivars. The maize improvement program at IITA has incorporated cutting-edge Omics and ICT tools to enhance genetic gains (Gedil et al., 2019). In the updated breeding strategy, molecular tools are integrated throughout the breeding pipeline, starting from pre-breeding, with the initial and crucial step being the char acterization of germplasm.

2.6 Linking Farmer Preferences to Nutritional Quality

Preferences for maize and maize-based foods vary across Africa, highlighting the need for region-specific approaches rather than one-size-fits-all solutions (Smale et al., 2013). While research and development (R&D) policies in Africa primarily focus on enhancing agronomic traits such as yield and resistance to abiotic and biotic stresses, attributes like taste, colour, nutritional value, and suitability for traditional or innovative dishes often receive less attention than they warrant (Hebinck et al., 2015). The true measure of success in maize breeding lies in the demand for and adoption of new varieties by end users. Breeders design new varieties based on product profiles, which outline the essential traits and characteristics required for a variety to be successful. Since different stakeholders—including processors and consumers have diverse needs, multiple product profiles are necessary. Gaining a thorough understanding of maize users' preferences and incorporating this knowledge into breeding programs across SSA will help optimize research resources, enhance the adoption of improved maize varieties, boost nutrition, and cater to both traditional and modern food processing requirements. With Africa's population projected to double between 2010 and 2050 and urbanization expected to rise from one-third to more than half, these efforts will be crucial in meeting future food demands. As food security improves, consumer demand for quality traits will grow. Expanding the use of maize in food products can support the rural-to-urban transition by providing more nutritious options and enhancing processing efficiency. This is especially important because many maize varieties with improved agronomic traits face challenges in the value chain, such as variations in organoleptic preferences and processing requirements, which limit their adoption for food use (Muzhingi et al., 2008a; Nkhabutlane et al., 2014). Maize breeding strategies and improved processing techniques that are grounded in a deep understanding of user preferences and nutritional needs could help meet daily dietary requirements while also strengthening the impact of breeding programs in developing countries.

One of the main barriers to integrating nutritional quality into breeding programs is the trade-off between agronomic performance and consumer acceptance (Gibson et al., 2018). Breeding strategies must ensure that nutritionally superior maize also meets processing, storage, and yield

stability requirements to be widely adopted. Furthermore, market awareness campaigns and policy incentives can play a significant role in encouraging the adoption of biofortified maize (Muzhingi et al., 2008). By aligning breeding objectives with farmers' needs, it is possible to develop maize varieties that are both nutritionally beneficial and agronomically viable.

The success of nutritionally improved maize varieties depends on their alignment with farmers' preferences, consumer demand, and agronomic performance. While biofortification offers a promising solution to malnutrition, its impact can only be maximized if breeding programs incorporate farmers' priorities. This study examines farmer preferences for maize and contextualises in this with respect to nutritional quality, by examining protein content of farmer-saved seed. The research did not consider the specific needs of each country in SSA; instead, maize production and consumption in Ilorin South LGA where maize is a staple food.

2.7 Materials & Methods

2.7.1 Study Area

This study adopted a mixed-method research design, integrating a field-based component conducted in Ilorin, Kwara State, Nigeria, with an experimental component carried out at the University of Essex, United Kingdom. The field study focused on assessing smallholder farmer preferences and perceptions of maize varieties, as well as collecting maize kernel samples for nutritional (protein content) analysis. The experimental study investigated the nutritional composition. This approach provided a holistic understanding of how social perceptions and environmental stress interact to affect maize nutritional quality and food security outcomes.
The field study was conducted in Ilorin, Kwara State, Nigeria (8°29′ N, 4°33′ E), a region situated in the southern Guinea savannah zone of the country. The area experiences a tropical climate with a mean annual rainfall of approximately 1,200 mm and temperatures ranging from 25°C to 32°C (Nigerian Meteorological Agency, 2022). Maize is one of the dominant staple crops grown in this area, cultivated primarily by smallholder farmers for household consumption and local market sales.

2.7.2 Small holder farmer survey

The social data used in this study were collected directly from smallholder farmers through structured questionnaire surveys administered during farm visits in Kwara State, Nigeria. Data collection was conducted by the researcher in the course of professional duties as an Agricultural Extensionist with MBS Global Goldenlinks Concepts, Ilorin. Prior to commencing the study, ethical approval was obtained from MBS Global Goldenlinks Concepts, which granted permission for the research to be undertaken. A copy is attached in the appendix. All participants were informed about the purpose of the study and voluntarily provided informed consent before participation. To protect respondents' privacy and confidentiality, all data were anonymised prior to analysis and reporting.The survey instrument was developed based on factors identified in previous studies as influencing maize variety selection, seed adoption, agricultural technology uptake, food security, and crop diversification among smallholder farmers in Sub-Saharan Africa (e.g., Langyintuo et al., 2010; Fisher et al., 2015; Abate et al., 2017). Questions covered maize varietal preferences, seed sources, food security perceptions, participation in government and non-government agricultural programmes, farming practices, indigenous knowledge, resource constraints, and perceived barriers to improving maize production and crop biodiversity. These themes were included because previous research has demonstrated their importance in shaping farmer decision-making and adoption behaviour.
The survey was informed by the Theory of Planned Behaviour (Ajzen, 1991), which proposes that behaviour is influenced by attitudes, subjective norms, and perceived behavioural control. Variables relating to varietal preferences, nutritional perceptions, and food security beliefs

were considered indicators of attitudes; participation in agricultural programmes and information networks reflected subjective norms; while resource availability, seed access, and perceived production constraints represented aspects of perceived behavioural control. This framework provided a theoretical basis for understanding the factors influencing maize variety selection and management decisions among smallholder farmers.

A limited number of Likert-scale items were included to assess selected farmer perceptions. Although longer scales are often recommended for measuring complex behavioural constructs, shorter scales are frequently employed in agricultural field surveys to minimise respondent burden, particularly in rural settings where interview duration and literacy considerations may affect data quality. Consequently, the Likert-scale items were used as indicative measures of farmer perceptions and were interpreted alongside descriptive survey responses rather than as comprehensive psychometric assessments.

Smallholder farmers were identified in Ilorin South Local Government Area of Kwara State, Nigeria, based on characteristics commonly associated with small-scale farming systems. These included the use of traditional farm implements, relatively small farm sizes, and a reliance on family labour for maize production. Identification of eligible participants was facilitated through agricultural extension officers, community leaders, and organised farmer groups within the study area. Their involvement helped ensure that respondents were actively engaged in smallholder maize production and broadly representative of local farming practices.

Participation in the study was entirely voluntary. Farmers were approached through face-to-face visits to their farms and, where appropriate, their homes. The purpose of the research was explained prior to data collection, and informed consent was obtained before interviews commenced. Participants were informed that the study sought to improve understanding of maize production, crop diversity, and food security, and that the findings would contribute to efforts aimed at addressing food security challenges within farming communities.

The survey was administered through in-person interviews. To ensure comprehension and accurate responses, questions were translated and explained in the local language when necessary, particularly for farmers with limited formal education. This approach facilitated effective communication and enhanced the reliability and completeness of the data collected.

2.7.3 Survey Design and Data Collection

A structured questionnaire was designed and administered to 20 smallholder maize farmers in Ilorin South Local Government Area of Kwara State, Nigeria. The questionnaire was developed to investigate the socioeconomic, institutional, and behavioural factors influencing the adoption and management of diverse maize varieties.

The questionnaire consisted primarily of closed-ended questions, supplemented by a small number of open-ended questions that allowed respondents to elaborate on their experiences, challenges, and perceptions. Survey questions were organised into six broad themes: (i) maize varietal diversity and seed sources, (ii) market influences on varietal selection, (iii) farmer knowledge and perceptions of nutritional benefits, (iv) participation in agricultural support programmes, (v) farming practices and indigenous knowledge, and (vi) constraints and support needs relating to maize production and crop biodiversity.

Data were collected through face-to-face interviews conducted on respondents' farms and, where necessary, in their homes. Responses were recorded during the interviews and subsequently organised for analysis. A copy of the complete questionnaire is provided in Appendix.

2.7.4 Determination of kernel protein content

Above-describe maize kernel samples were ground using a manually operated coffee bean grinder. Ground samples were precisely weighed (0.5 mg +/- 10%) into individual tin capsule and sent to The Goodwin Laboratory for Paleoclimate Research (Cambridge, UK) for analyses of nitrogen content. Samples were analyzed for percentage nitrogen using a Costech Elemental Analyzer coupled with a Thermo DELTA V mass spectrometer via a Conflo IV in continuous flow mode. The samples underwent flash combustion in a reactor at 1500°C within an oxygen-enriched atmosphere. The resulting elemental components were carried by helium through an oxidation catalyst (chromium trioxide and silver-coated cobaltic oxide) at 1020°C, with excess oxygen removed in a reduction tube containing metallic copper at 650°C. Water vapour is eliminated using magnesium perchlorate, and the gases were then separated in a gas chromatographic column at 45 ± 0.1°C. The separated gases were analyzed by the mass spectrometer. The area under the peak for nitrogen was used to measure the percentage of nitrogen. The precision of this analysis is ±0.5%. Total protein content was calculated by multiplying the percentage of kernel nitrogen on a mass basis by 6.25 (Mariotti et al. (2008)).

2.7.5 Data and statistical analyses

Survey data obtained from the smallholder farmer questionnaires were coded and entered in R statistical software for analysis. Descriptive statistics, including frequencies and percentages, were used to summarise farmer socio-economic characteristics, maize variety adoption patterns, seed sources, market participation, and perceptions related to nutrition, crop biodiversity, and food security. Survey results were presented using tables and graphical summaries where appropriate.

Laboratory measurements of nitrogen content (%) in maize grain samples were used to estimate protein content. Crude protein content was calculated by multiplying the percentage nitrogen by a conversion factor of 6.25, based on the assumption that proteins contain approximately 16% nitrogen. Protein content was calculated using the following equation:

$$Protein\ (\%) = Nitrogen\ (\%) \times 6.25$$

The calculated protein values were grouped according to maize type (white, yellow, and red) and summarised using descriptive statistics, including mean and standard deviation.

To determine whether protein content differed significantly among maize types, a one-way Analysis of Variance (ANOVA) was performed using maize type as the explanatory variable and protein content as the response variable. A second one-way ANOVA was conducted to assess whether protein content differed significantly among sampling locations. To evaluate the combined influence of maize type and sampling location on protein content, a two-way ANOVA was subsequently performed, with maize type and location included as fixed factors together with their interaction term (maize type × location). Statistical significance was assessed at $p < 0.05$.

Associations between farmer preference for white maize and categorical explanatory variables, including perceived market demand, seed source, nutritional awareness, participation in government or NGO programmes, and maize marketing status, were examined using Fisher's Exact Test because of the small sample size and low expected cell frequencies.

Differences in farmers' preferences for white and yellow maize were assessed using the McNemar test, while a chi-square goodness-of-fit test was used to compare the observed

frequencies of white and yellow maize preferences.

A binary logistic regression model was fitted to evaluate whether perceived market demand, drought perception, seed source, nutritional awareness, and participation in government or NGO programmes predicted farmers' preference for white maize. Results were reported as odds ratios with corresponding statistical significance. Results from the statistical analysis of protein content were interpreted alongside survey findings to provide an integrated assessment of the relationship between smallholder farmer preferences, maize variety selection, and nutritional quality.

2.8 Results

2.8.1 Variety Distribution Patterns

White maize was the most widely cultivated maize type among surveyed farmers, accounting for 44.7% of reported varieties grown, followed closely by yellow maize (42.1%), while red maize represented only 13.2% of cultivation (Figure 5). The distribution of maize varieties varied across the surveyed communities. White maize was the dominant variety in several locations, including Tanke, Gudugba, and Gaa Akanbi. Yellow maize was also widely cultivated and showed relatively high representation in communities such as Gudugba and Tanke. In contrast, red maize was cultivated by a smaller proportion of farmers and was primarily reported in communities including Alade, Alalubosa, and Omode. These results indicate that while white maize remains culturally dominant, yellow maize is gaining recognition due to awareness of its nutritional and drought-resistant qualities.

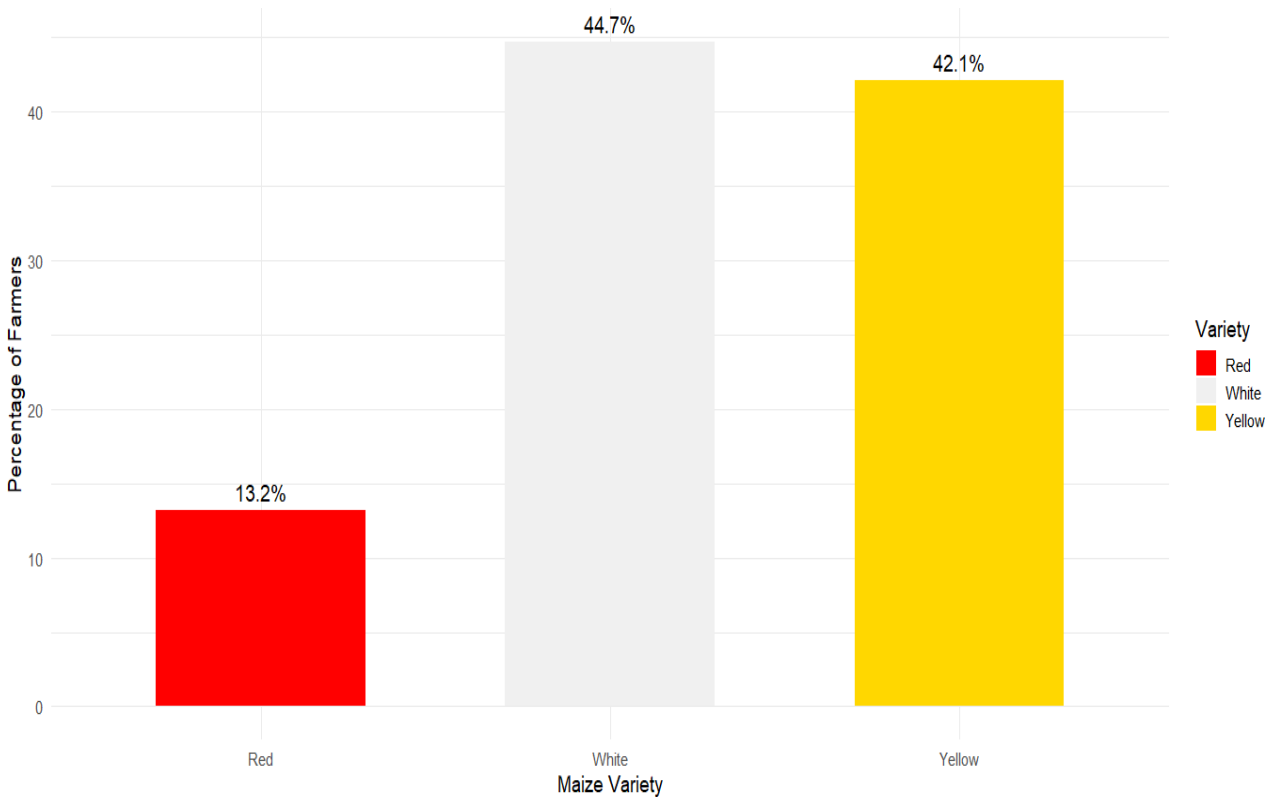


Figure 5. Proportion of surveyed farmers growing different maize varieties in Ilorin South, Nigeria. Bar chart showing the percentage of farmers reporting cultivation of red, white, and

yellow maize varieties. White maize was the most widely grown variety (44.7%), followed closely by yellow maize (42.1%), while red maize was grown by a smaller proportion of farmers (13.2%). Percentages are based on farmer self-reports collected through a structured questionnaire survey and reflect varietal presence rather than area planted or yield contribution.

Farmers' selection of maize varieties appears to reflect perceived trade-offs rather than absolute performance. Decisions are influenced by multiple considerations, including yield potential, drought tolerance, grain quality, and culinary or market acceptability. Although cultivated by relatively few farmers, red maize persists in specific communities, suggesting niche uses, cultural significance, or local adaptation.

2.8.2 Seed Sources and Access

The findings show a high reliance on farm-saved seed among smallholder farmers in Ilorin South, with over 60% of respondents reusing seed from their own harvest. This indicates that on-farm seed saving remains the dominant seed source in the study area. In addition to saved seed, nearly 40% of farmers obtain seed from external sources. These include government programmes and, to a lesser extent, informal exchange and market channels, indicating the presence of both formal and informal seed sourcing systems within the study area.

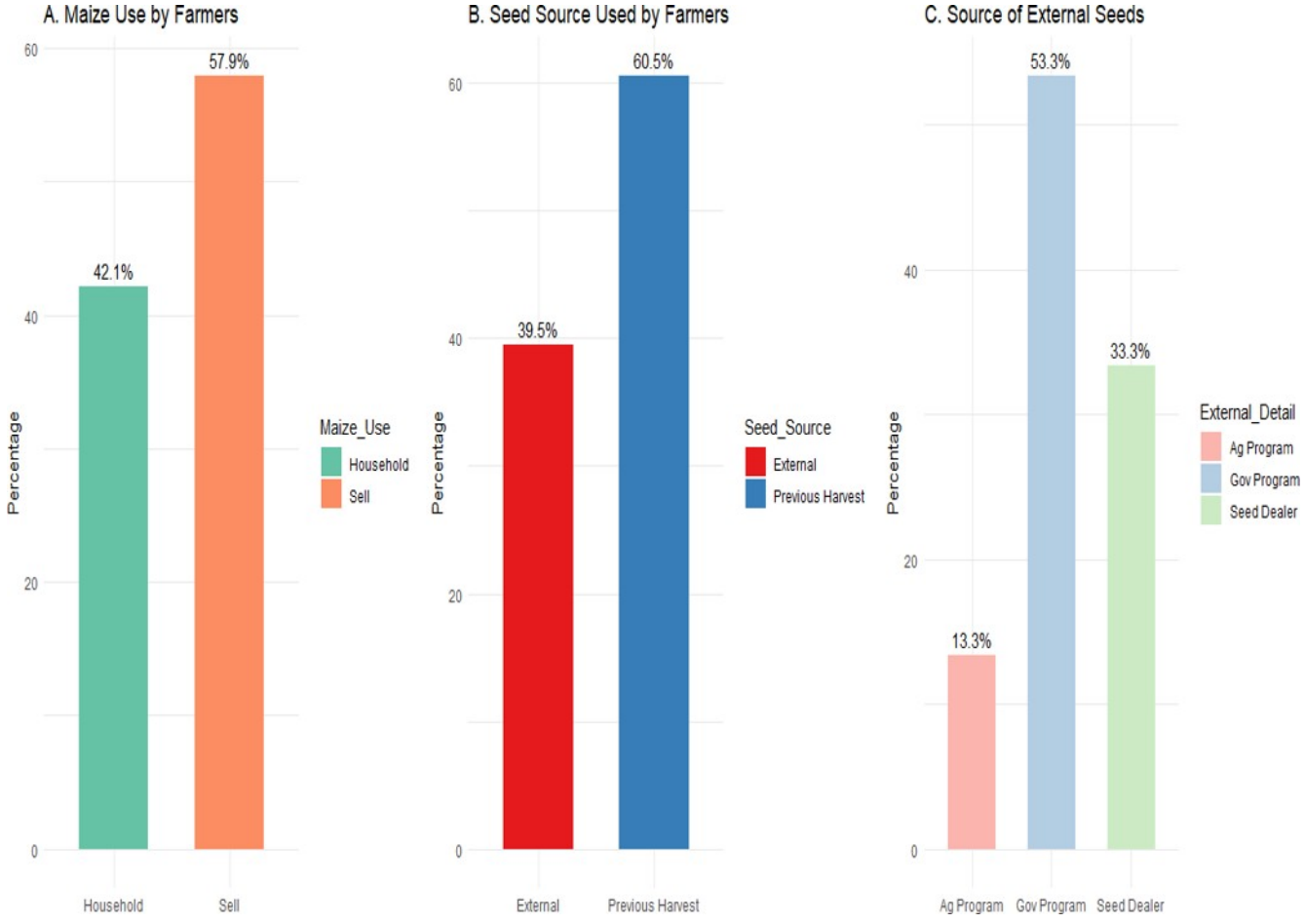


Figure 6. Seed use and seed sourcing pathways among surveyed maize farmers in Ilorin South, Nigeria. (A) Proportion of farmers reporting maize production primarily for household

consumption or for sale. (B) Proportion of farmers obtaining seed from saved seed from previous harvests versus external sources. (C) Breakdown of external seed sources, including government programmes, agricultural projects, and seed dealers. Percentages are based on farmer self-reports collected through a structured questionnaire and reflect reported practices rather than quantities of seed used or area planted.

2.8.3 multi-variety cultivation in Practices

The findings show a near-universal adoption of multi-variety maize cultivation among farmers in the study area. Most farmers reported growing more than one maize variety within the same farming season or across seasons, indicating that varietal diversification is a common practice in the study population.

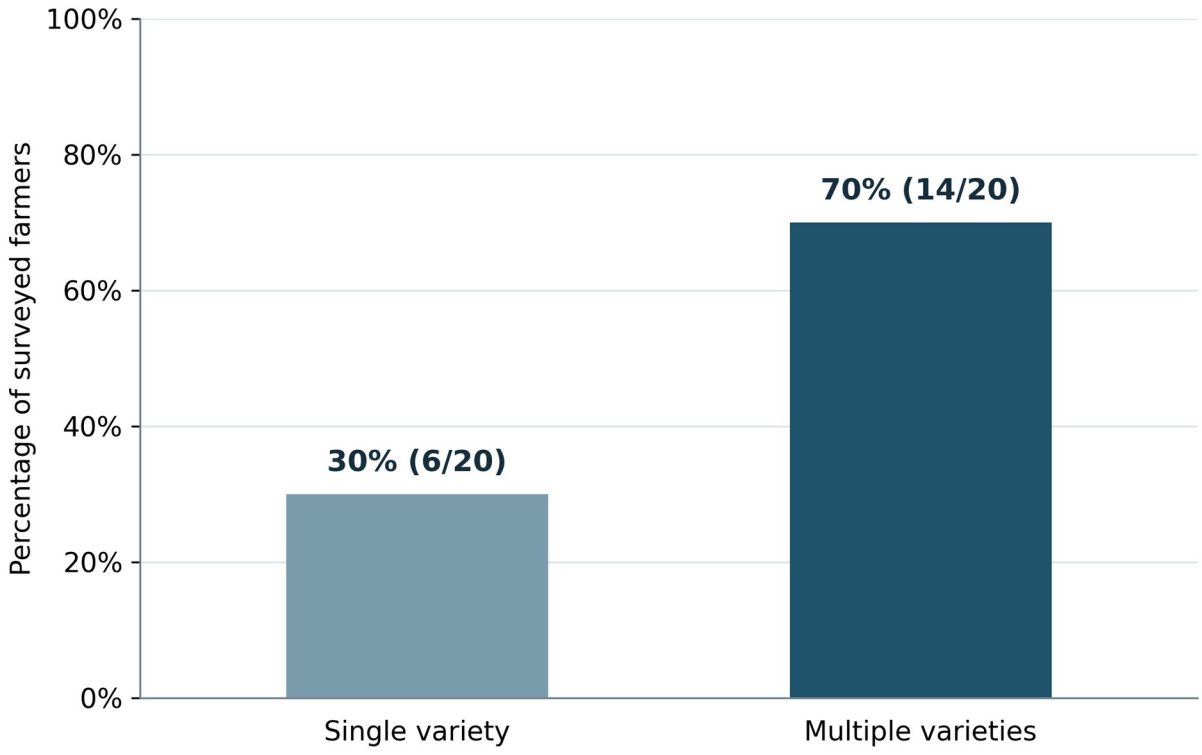


Figure 7. Prevalence of multi-variety versus single-variety maize cultivation among surveyed farmers in Ilorin South, Nigeria. Bar chart showing the percentage of farmers reporting cultivation of more than one maize variety (multi-variety) compared with those growing a single maize variety. The majority of farmers (70%) reported multi-variety cultivation, while only a small proportion (30%) relied on a single variety. Percentages are based on farmer self-reports collected through a structured questionnaire survey.

2.8.4 Farmer Preferences and Market Influence

The survey indicated that white maize remains the most widely cultivated and preferred variety (44.7%), followed closely by yellow maize (42.1%) and red maize (13.2%). Spatial analysis of varietal distribution showed variation across communities. White maize was dominant in most surveyed locations, while yellow maize also showed substantial representation across several communities. Red maize was cultivated by a smaller proportion of farmers and was mainly

found in specific or limited locations, indicating its minor role in overall production.

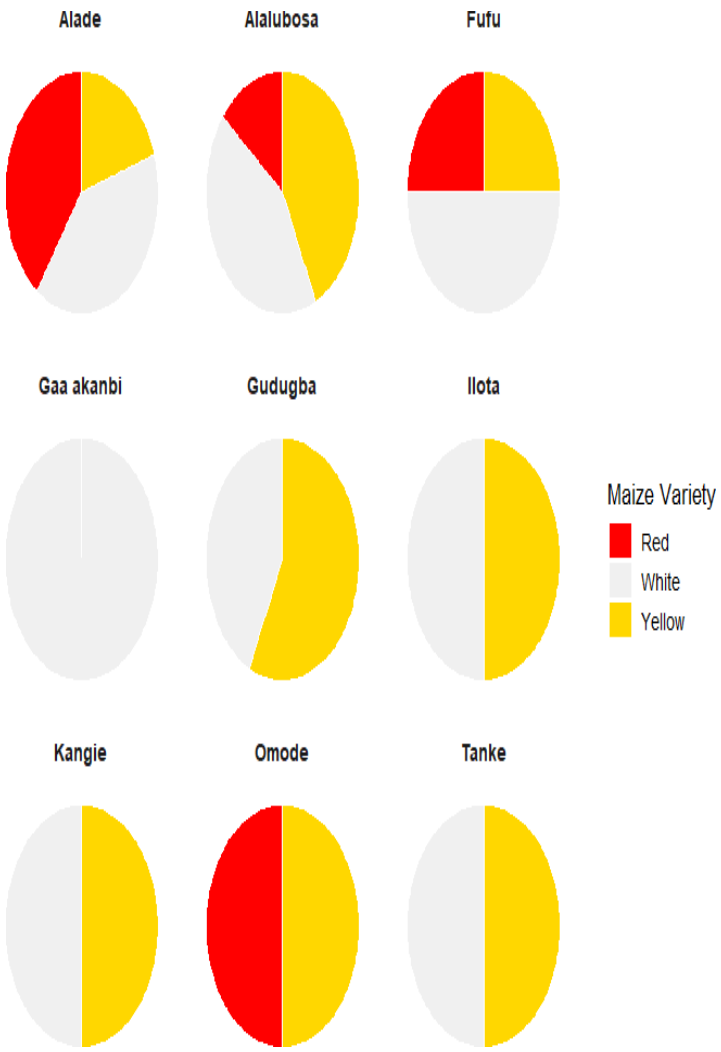


Figure 8. Spatial variation in maize variety cultivation across surveyed communities in Ilorin South, Nigeria. Pie charts showing the proportion of red, white, and yellow maize varieties grown in each surveyed community (Alade, Alalubosa, Fufu, Gaa Akanbi, Gudugba, Ilota, Kangie, Omode, and Tanke). Each pie represents a single community and illustrates local differences in varietal composition, highlighting heterogeneity in maize cultivation patterns across the study area. Data are based on farmer self-reports collected through a structured questionnaire survey.

2.8.5 Protein content of maize grain

Analysis of maize samples collected from farmers' fields in Ilorin South revealed variation in protein content among maize types and across locations. Descriptive results showed that white maize generally had the lowest protein concentrations; yellow maize consistently exhibited higher protein levels, and red maize displayed intermediate values.

One-way ANOVA indicated that maize type had a highly significant effect on protein content ($F = 15.86$, $p < 0.001$), confirming that varietal identity influences nutritional quality. Location also had a significant effect on protein content ($F = 3.14$, $p = 0.013$), suggesting that site-specific factors contribute to variation in grain quality.

Two-way ANOVA further showed that maize type and location independently affected protein content ($p < 0.001$), while their interaction was not significant ($p = 0.425$), indicating that differences among maize types were consistent across all sampled locations.

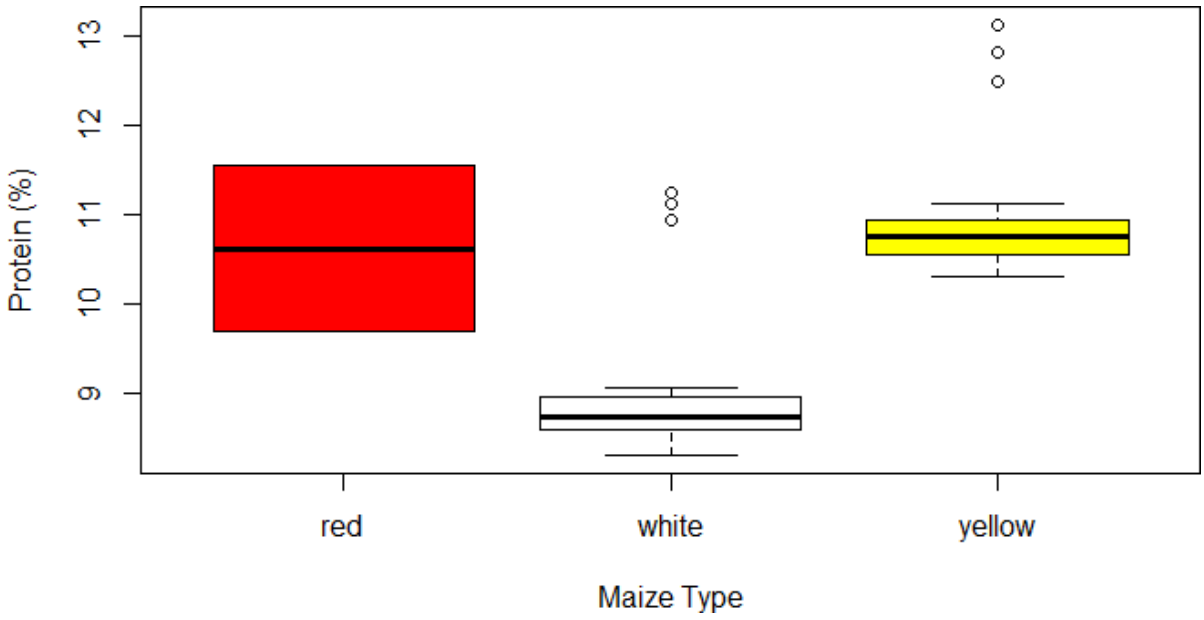


Figure 9. Grain protein content of different maize types grown by surveyed farmers in Ilorin South, Nigeria. Boxplots showing the distribution of grain protein content (%) for red, white, and yellow maize types. Boxes represent the interquartile range with median values indicated by horizontal lines; whiskers denote the range excluding outliers, which are shown as individual points. Differences in protein content between maize types highlight variation in the nutritional quality of commonly cultivated maize, with potential implications for dietary protein intake in maize-dependent households.

2.8.6 Factors Influencing Preference for White Maize

Several farmer- and market-related factors were examined to determine whether they were associated with preference for white maize. These included perceived market demand, source of seed, awareness of nutritional differences between maize varieties, participation in government or non-governmental organisation (NGO) agricultural programmes, and maize marketing status. Given the relatively small sample size and the presence of small cell frequencies in several of the contingency tables, Fisher's Exact Test was used to assess the statistical significance of the associations. The results indicated that none of the factors examined were significantly associated with preference for white maize at the 5% significance level.

2.8.6.1 Influence of Market Demand on Preference for White Maize

The relationship between farmers' perceptions of market demand and their preference for white maize was examined using Fisher's Exact Test. Respondents were categorized according to whether they considered market demand to be unimportant, somewhat important, or very important in relation to their choice of maize variety.

Among the respondents who considered market demand to be unimportant, five farmers preferred white maize, while six did not. Among those who considered market demand to be

somewhat important, four farmers preferred white maize and four did not. Only one respondent considered market demand to be very important, and this respondent reported a preference for white maize. Overall, the distribution of white maize preference was relatively similar across the different levels of perceived market demand.

Fisher's Exact Test showed that there was no statistically significant association between perceived market demand and preference for white maize ($p = 1.000$). Therefore, within the surveyed sample, the level of importance attached to market demand was not significantly associated with whether farmers preferred white maize. Although the descriptive results show that the only respondent who considered market demand very important preferred white maize, the small number of respondents in this category limits the extent to which this pattern can be interpreted.

2.8.6.2 Influence of Seed Source on Preference for White Maize

Seed source was also examined as a potential factor associated with preference for white maize. The sources of seed reported by respondents included government agricultural programmes, saved seed, commercial or independent seed dealers, and other sources. The analysis considered whether farmers obtaining seed through different sources differed in their reported preference for white maize. Farmers who obtained seed through government programmes showed a similar pattern of preference for white maize to those obtaining seed through other sources. Preferences were also observed among farmers who relied on saved seed and those who obtained seed from seed dealers or other sources. Thus, there was no clear descriptive pattern suggesting that obtaining seed from a particular source was associated with a greater likelihood of preferring white maize.

Fisher's Exact Test indicated that the association between seed source and preference for white maize was not statistically significant ($p = 0.614$). This finding suggests that, within the study population, the reported source from which farmers obtained maize seed was not significantly associated with their preference for white maize.

2.8.6.3 Influence of Nutritional Awareness on Preference for White Maize

Farmers' awareness of nutritional differences between maize varieties was assessed to determine whether nutritional knowledge was associated with preference for white maize. Respondents were divided into two groups according to whether they reported awareness of nutritional benefits or differences associated with different maize varieties. Among respondents who were not aware of nutritional differences between maize varieties, five preferred white maize and six did not. Among respondents who reported awareness of nutritional differences, five preferred white maize while four did not. The proportion of respondents preferring white maize was therefore broadly similar between the two awareness groups.

Fisher's Exact Test showed no statistically significant association between nutritional awareness and preference for white maize ($p = 1.000$). Thus, the results did not provide statistical evidence that awareness of nutritional differences between maize varieties was associated with preference for white maize in the surveyed population. Although the descriptive frequencies suggest a slightly higher proportion of white maize preference among respondents who were aware of nutritional differences, this difference was not statistically significant.

2.8.6.4 Influence of Participation in Government or NGO Programmes

Participation in government or NGO agricultural programmes was also considered a potential factor associated with maize varietal preference. Respondents were classified according to whether they had participated in a government or NGO agricultural programme. All three respondents who reported participation in a government or NGO programme preferred white maize. In comparison, among the seventeen respondents who had not participated in such programmes, seven preferred white maize while ten did not. Descriptively, therefore, the proportion of respondents preferring white maize was higher among those who had participated in agricultural programmes.

However, the number of respondents who had participated in such programmes was small. Fisher's Exact Test produced a p-value of 0.211, indicating that the association between programme participation and preference for white maize was not statistically significant. Consequently, despite the descriptive difference observed between the two groups, the analysis did not provide sufficient statistical evidence to conclude that participation in government or NGO agricultural programmes was associated with preference for white maize.

2.8.6.5 Influence of Maize Marketing on Preference for White Maize

The relationship between maize marketing status and preference for white maize was also examined. Respondents were classified according to whether they reported selling maize.

Among respondents who did not sell maize, seven preferred white maize while five did not. Among respondents who sold maize, three preferred white maize while five did not. Descriptively, white maize preference was therefore more common among respondents who did not sell maize than among those who reported selling maize.

However, Fisher's Exact Test showed that the association between maize marketing status and preference for white maize was not statistically significant ($p = 0.650$). Therefore, the results did not provide evidence of a statistically significant relationship between whether farmers marketed their maize and their preference for white maize.

Overall, the findings from the individual association tests indicate that none of the examined factors perceived market demand, seed source, nutritional awareness, participation in government or NGO programmes, or maize marketing status was significantly associated with preference for white maize. Although some descriptive differences were observed between groups, these differences did not reach statistical significance.

2.8.7 Comparison of White and Yellow Maize Preferences

A comparison was made between farmers' preferences for white and yellow maize to determine whether respondents demonstrated a statistically significant preference for one of the two maize types. Because the comparison involved paired responses from the same respondents, a McNemar test was conducted to assess whether there was a significant difference between the number of respondents preferring white maize and those preferring yellow maize.

The McNemar test showed no statistically significant difference between preference for white and yellow maize (McNemar's $\chi^2 = 0.00$, $p = 1.000$). This result indicates that the paired responses did not demonstrate evidence of a systematic preference for one variety over the other.

A separate chi-square goodness-of-fit test was also conducted using the observed numbers of mentions for white maize and yellow maize. White maize was mentioned by 10 respondents, compared with 11 respondents for yellow maize. The difference between these frequencies was very small. The chi-square goodness-of-fit test confirmed that the difference was not statistically significant ($\chi^2 = 0.048$, df = 1, $p = 0.827$).

Taken together, the two analyses indicate that the surveyed farmers did not show a statistically significant difference in preference between white and yellow maize. Although yellow maize was mentioned slightly more frequently than white maize in the goodness-of-fit analysis, the difference was too small to provide statistical evidence of a preference for either maize type. Therefore, the results suggest broadly comparable levels of reported preference for white and yellow maize within the study sample.

2.8.8 Logistic Regression Analysis

A binary logistic regression analysis was conducted to further examine whether the factors considered in the preceding analyses could predict preference for white maize when considered simultaneously. Preference for white maize was specified as the binary outcome variable, while market demand, drought perception, seed source, nutritional awareness, and participation in government or NGO programmes were included as explanatory variables.

The logistic regression analysis showed that none of the explanatory variables was a statistically significant predictor of preference for white maize ($p > 0.05$ for all variables). Thus, when the variables were considered together within the regression model, there was no statistically significant evidence that any of the measured factors independently predicted whether a respondent preferred white maize.

Nutritional awareness produced an odds ratio close to 1.0, indicating that the odds of reporting a preference for white maize were similar between respondents with and without reported nutritional awareness, after accounting for the other variables included in the model. Similarly, market demand did not emerge as a significant predictor of white maize preference. The same pattern was observed for drought perception, seed source, and participation in government or NGO programmes, none of which demonstrated a statistically significant predictive relationship with the outcome.

The logistic regression findings were consistent with the results of the individual association tests presented in Section 2.8.6. In both the univariate analyses and the multivariable model, there was no statistically significant evidence that the examined farmer, market, nutritional, or programme-related factors were associated with preference for white maize.

Overall, the results suggest that preference for white maize was not significantly predicted by the variables included in the regression model. The absence of statistically significant predictors should, however, be interpreted in the context of the relatively small sample size, which may limit the statistical power of the analysis to detect associations. The findings therefore indicate that no significant associations were detected within the surveyed sample rather than demonstrating that these factors cannot influence maize varietal preferences more broadly.

2.9 Discussion

2.9.1 Variety Distribution Patterns and Farmer Decision-Making

The strong predominance of white maize across the surveyed communities reflects the continued influence of cultural traditions, culinary preferences, and long-established consumption patterns. White maize remains the preferred staple for household consumption and food processing, reinforced by consistent market demand where consumers favour white grain. Similar patterns have been widely reported across West Africa, where white maize dominates human consumption, while yellow maize is often associated with livestock feed, particularly poultry (MoFA-SRID, 2010; 2012). Studies across sub-Saharan Africa also confirm a persistent preference for white maize among both farmers and consumers (De Groote et al., 2002; Stevens and Winter-Nelson, 2008; Sibiya et al., 2013). This preference is largely rooted in familiarity and long-standing consumption habits, with grain colour often serving as a perceived indicator of quality (Ranum et al., 2014). Conversely, yellow maize has historically been associated with food aid, animal feed, or lower social status, which has limited its acceptance for human consumption in many contexts. Differences in taste and perceived culinary suitability have further reinforced this bias (Ranum et al., 2014). Collectively, these factors demonstrate that cultural acceptability and consumer preference continue to strongly shape production decisions, often outweighing agronomic or nutritional considerations.

Despite this dominance, the relatively substantial cultivation of yellow maize across the study area is noteworthy. Its presence suggests gradual integration of improved or hybrid varieties into farming systems, likely driven by perceived agronomic and economic benefits. Previous studies indicate that adoption of yellow maize in sub-Saharan Africa is often associated with higher yield potential, improved drought tolerance, and expanding market demand from feed and processing industries (De Groote et al., 2016; Simtowe et al., 2019). Furthermore, biofortification initiatives promoting provitamin A–enriched maize have increased farmer exposure through extension services, seed programmes, and policy interventions (HarvestPlus, 2014). The observed pattern in Ilorin South therefore reflects a gradual shift in farmer priorities, where traditional preferences for white maize are increasingly balanced with practical responses to environmental stress, market opportunities, and improved seed access. This indicates that varietal preference is dynamic and shaped by evolving socio-economic and institutional conditions.

Farmers' selection of maize varieties in the study area reflects trade-offs among multiple criteria rather than reliance on a single performance indicator. Decisions are shaped by yield potential, drought tolerance, grain quality, and market or culinary acceptability. Consequently, varieties that perform adequately under stress while meeting consumption and market expectations are often preferred over those with superior agronomic performance but limited acceptability. This highlights the complexity of smallholder decision-making processes in varietal choice.

The continued cultivation of red maize, although limited, suggests the existence of niche functions such as cultural significance, local adaptation, or specialised uses. Its persistence underscores the importance of minor crops within diversified smallholder systems, where genetic and functional diversity contributes to resilience and livelihood strategies.

Perceptions linking yellow maize with drought tolerance are consistent with studies showing its frequent association with improved or hybrid varieties (De Groote et al., 2016; Simtowe et al., 2019). The yellow pigmentation, due to carotenoids, may also influence sensory attributes

such as taste and aroma, thereby shaping farmer and consumer evaluation (Tomlins et al., 2012). These experiential perceptions are developed through repeated observation of crop performance under variable environmental conditions and play a role in shaping on-farm selection decisions (Soleri & Cleveland, 2009). However, physiological evidence indicates that drought tolerance is primarily determined by traits such as root architecture, stomatal regulation, and water-use efficiency rather than grain colour (Tardieu, 2012). This highlights the need to interpret farmer perceptions as context-specific knowledge systems rather than direct indicators of physiological performance. Integrating local knowledge with scientific evidence therefore provides a more complete understanding of varietal choice and adaptation in smallholder maize systems.

2.9.2 Seed Sources and Access

The dominance of farm-saved seed in this study challenges narratives suggesting that smallholder farmers are now primarily dependent on off-farm seed sources. While some studies argue that external channels such as markets and social networks dominate seed su pply, even during periods of stress (De Waal, 1991; Cavatassi et al., 2011; Guei et al., 2011), the present findings show that on-farm seed saving remains a central and rational strategy in Ilorin South. This aligns with evidence that informal seed systems persist where formal seed markets are weak, distant, or unaffordable (Bezner Kerr, 2013; Marfo et al., 2008).

Farmers' preference for saved seed reflects practical considerations, including reduced cost, guaranteed availability, and the use of locally adapted varieties with known performance. This behaviour does not indicate resistance to innovation but rather reflects structural constraints such as limited access to certified seeds, inconsistent supply, and financial risk. Seed saving therefore represents an adaptive response to local socio-economic and institutional conditions. The presence of nearly 40% of farmers accessing external seed sources, particularly through government programmes, highlights the importance of public intervention in strengthening seed access. This level of engagement is relatively higher than findings from multi-country studies, where reliance on formal seed systems has been reported to be very low, sometimes below 3% (McGuire & Sperling, 2016). This suggests that institutional support in Ilorin South plays a comparatively more active role in seed distribution.

However, continued reliance on saved seed may slow the turnover of varieties and limit the uptake of improved traits such as drought tolerance and enhanced nutritional quality. At the same time, this pattern reflects constrained choice rather than lack of awareness, as farmers balance the benefits of continuity with selective adoption of external seed when conditions allow. Overall, seed sourcing in the study area reflects adaptive capacity shaped by access, risk, and context. It demonstrates that seed systems are dynamic and multi-sourced, where formal and informal channels coexist. This underscores the need for breeding and extension programmes to align more closely with farmer realities and the practical constraints influencing seed decisions.

2.9.3 multi-variety cultivation as a risk management strategy

The widespread adoption of multi-variety maize cultivation supports a well-established body of literature describing varietal diversity as a deliberate and rational risk management strategy in smallholder farming systems. Farmers maintain multiple crop varieties as a form of on-farm conservation, enhancing adaptation to agroecological variability such as fluctuating rainfall patterns, soil differences, and pest pressures (Ceccarelli, 1996; Di Falco and Chavas, 2009; Worthington et al., 2012).

In rainfed agricultural systems, where production shocks can have severe livelihood consequences, varietal diversification is widely recognised as a strategy that prioritises yield stability and resilience rather than maximising the performance of a single cultivar (Di Falco and Perrings, 2005; Cavatassi et al., 2011). This explains the high prevalence of multi-variety cultivation observed in the study area. Beyond risk reduction, the use of multiple maize varieties allows farmers to meet diverse household and economic objectives simultaneously. These include household consumption needs, market demand, and cultural or culinary preferences, consistent with findings from other smallholder farming contexts (Brush, 1992; King, 2007; Keleman et al., 2013). This demonstrates that varietal diversification is both an economic and socio-cultural strategy.

However, while on-farm diversity enhances resilience, existing literature also highlights that reliance on predominantly local and informal seed systems may limit access to a wider pool of improved or stress-tolerant germplasm (Bellon et al., 2011; Isakson, 2011; Pautasso et al., 2013). This tension is also reflected in the present study, where farmers' diversification strategies provide stability but may inadvertently restrict exposure to newer varieties with enhanced agronomic traits.

Overall, the findings align with theoretical and empirical evidence showing that risk aversion is a key driver of crop diversity in smallholder systems. Farmers intentionally maintain varietal diversity as a hedge against environmental and economic uncertainty, resulting in agroecosystems that are resilient but often locally constrained in terms of genetic exchange and innovation (Di Falco and Perrings, 2003).

2.9.4 Farmer Preferences and Market Influence

The dominance of white maize reflects long-established consumer preferences, cultural beliefs, and strong market demand, particularly for staple food preparation. These findings are consistent with extensive literature from West and sub-Saharan Africa, which documents the predominance of white-endosperm maize due to its culinary suitability, processing qualities, and entrenched cultural acceptance (De Groote et al., 2002; Stevens & Winter-Nelson, 2008; Ranum et al., 2014). Market actors also reinforce this preference by offering more stable demand and better price reliability for white grain, highlighting the combined influence of socio-cultural and economic factors in shaping varietal dominance alongside agronomic considerations.

The substantial presence of yellow maize both supports and extends existing literature. Traditionally, yellow maize has been less preferred for human consumption in many African contexts and more commonly associated with livestock feed or food aid (Ranum et al., 2014). However, recent studies indicate increasing acceptance of yellow maize, particularly where awareness of its provitamin A content has expanded and where improved or hybrid varieties are promoted through extension services and public health interventions (Meenakshi et al., 2012; De Groote et al., 2016). The observed proportion of yellow maize in this study therefore suggests that varietal preferences are dynamic and influenced by changing nutritional awareness, perceived agronomic advantages such as drought tolerance, and exposure to improved germplasm rather than being solely shaped by tradition.

Varietal preference should therefore be understood as transitional rather than fixed. Farmers continuously adjust planting decisions in response to social, economic, and environmental signals, demonstrating flexible risk management strategies. This is reflected in the balance

between household consumption needs and market-oriented production, where white maize is often prioritised for staple food use while yellow maize is increasingly incorporated for its perceived agronomic or nutritional advantages. Such dual-purpose decision-making highlights the multidimensional nature of varietal choice in smallholder systems.

Spatial variation in maize distribution further underscores the context-specific nature of varietal adoption. Differences across communities suggest that local seed availability, agroecological conditions, market access, and cultural norms all interact to shape planting decisions. While stated preferences do not always translate directly into actual cultivation due to constraints such as seed access or environmental variability, they remain important indicators of farmer priorities. Together, these findings provide a contextual foundation for understanding subsequent discussions on nutritional quality and drought response.

2.9.5 Protein content of maize grain

Grain protein content is a key nutritional trait in maize-based diets, particularly in regions such as Nigeria where maize is a staple food and a major source of dietary protein. In households with limited access to diverse proyield and stress tolerance in maize evaluation.

The findings are consistent w tein sources, even small differences in maize protein content can have important implications for nutrition, especially among vulnerable populations. This highlights the importance of considering nutritional quality alongside ith studies showing substantial genetic and environmental variation in maize grain protein content. Badu-Apraku et al. (2015) report significant variation among maize genotypes, with higher protein levels often associated with improved or nutritionally enhanced germplasm. Environmental conditions such as soil fertility and nitrogen availability also play a critical role in determining protein expression (Ortiz-Monasterio et al., 2007), supporting the observed significant effect of location in this study.

The relationship between protein content and farmer preferences is complex. Despite generally lower protein levels, white maize remains the most widely cultivated and preferred variety due to strong cultural attachment and market demand, a pattern widely documented in African maize systems (De Groote et al., 2002; Stevens & Winter-Nelson, 2008). In contrast, yellow maize, which exhibited higher protein levels in this study, has gained increasing attention in areas where its nutritional benefits—particularly provitamin A content—are promoted through public health campaigns and extension services (Meenakshi et al., 2012; De Groote et al., 2016). However, red maize remains marginal despite sometimes comparable nutritional characteristics, indicating that adoption is driven more by socio-cultural and economic factors than by nutritional superiority alone.

Multi-variety cultivation may help moderate the nutritional implications of these differences. By growing multiple maize types, households can diversify dietary protein sources and reduce reliance on a single nutritionally limited variety. This aligns with broader evidence that varietal diversity contributes not only to agronomic resilience but also to nutritional resilience (Bellon et al., 2011; Di Falco & Perrings, 2005). In this context, higher-protein varieties such as certain yellow maize lines may contribute to addressing micronutrient and protein deficiencies, although adoption depends on seed availability, cost, and compatibility with local farming systems.

It is also important to note that protein content alone does not fully represent nutritional quality, as protein composition, amino acid balance, and bioavailability also determine dietary value.

Nonetheless, the observed variation provides important insight into the intersection of varietal choice, seed systems, and household nutrition in smallholder maize production systems.

2.9.6 Factors Influencing Farmer Preference for White Maize

The results indicate that farmer preference for white maize was not significantly influenced by market demand, seed source, nutritional awareness, participation in agricultural programmes, or maize marketing status. Although white maize has traditionally been regarded as the preferred grain type in many parts of Sub-Saharan Africa, the findings suggest that preference patterns within the study area may be more complex than commonly assumed.

The absence of a significant relationship between nutritional awareness and preference for white maize is particularly noteworthy. This finding suggests that knowledge of nutritional benefits alone may not be sufficient to influence varietal choice. Farmers often make decisions based on multiple and interacting considerations, including familiarity, household consumption needs, grain characteristics, and perceived agronomic performance. Similar observations have been reported in studies showing that adoption decisions are influenced by a combination of social, cultural, economic, and production-related factors rather than by nutritional considerations alone (Marenya et al., 2021; Abera et al., 2020).

Likewise, the lack of association between seed source and varietal preference suggests that access to seed through formal or informal channels does not necessarily determine farmer's choice. Many smallholder farmers continue to rely on saved seed and local seed networks, selecting varieties that have demonstrated acceptable performance under local conditions. Such behaviour reflects the importance of experiential knowledge and local adaptation in shaping varietal decisions.

Although all respondents who had participated in government or NGO programmes preferred white maize, the relationship was not statistically significant. The small number of programme participants in the survey limits the ability to draw firm conclusions regarding programme effects. Nevertheless, the pattern may indicate an area worthy of further investigation using a larger sample size.

The comparison between white and yellow maize preferences revealed no significant difference between the two varieties. This finding is important because it suggests that yellow maize has achieved a level of acceptance comparable to white maize within the study area. Earlier studies frequently reported strong farmer and consumer preferences for white maize due to cultural familiarity and food preferences (De Groote et al., 2002; Stevens and Winter-Nelson, 2008). However, increasing awareness of the nutritional benefits of yellow maize, together with the promotion of improved and biofortified varieties, may be contributing to greater acceptance among farmers.

The logistic regression analysis further supported the conclusion that the socio-economic variables examined were poor predictors of preference for white maize. The large confidence intervals and unstable parameter estimates observed in the model likely reflect the relatively small sample size of twenty respondents and the limited number of observations within some categories. Consequently, the regression analysis should be viewed as exploratory rather than definitive. Future studies involving larger and more geographically diverse samples would provide greater statistical power to identify the factors that influence varietal preference among maize farmers.

Overall, the findings suggest that farmer preferences in Ilorin South are relatively balanced between white and yellow maize and are not strongly explained by the socio-economic variables investigated in this study. This highlights the need for maize improvement programmes to consider a broader range of behavioural, cultural, agronomic, and market-related factors when promoting nutritionally enhanced maize varieties.

3.0 Chapter three: Maize-water relations: Studies on genetic variation for drought tolerance and water use efficiency in maize

3.1 Introduction

Maize (Zea mays L.) is one of the world's most important cereal crops, serving as a major source of food, livestock feed, industrial raw materials, and household income for millions of people. Globally, maize contributes substantially to food security owing to its high productivity, adaptability to diverse agroecological conditions, and wide range of end uses. In Sub-Saharan Africa (SSA), maize is the principal staple crop for many rural households and provides a significant proportion of daily dietary energy and protein. Beyond its nutritional importance, maize production plays a vital role in supporting rural livelihoods through income generation, employment, and livestock production. Consequently, maintaining stable maize productivity is essential for achieving sustainable agricultural development and food security across the region. Despite its importance, maize production in many parts of SSA remains heavily dependent on rainfall and is therefore highly vulnerable to climatic variability.

Among the various environmental constraints affecting maize production, drought is recognized as one of the most significant factors limiting crop growth and grain yield. Climate change has increased both the frequency and severity of drought events, resulting in greater uncertainty in agricultural production and threatening the resilience of rain-fed farming systems (Cairns et al., 2013; Lobell et al., 2014; IPCC, 2023). The effects of drought are particularly severe during sensitive developmental stages such as flowering and grain filling, when water deficits can substantially reduce kernel set and final grain yield. Consequently, improving drought tolerance has become a major priority in global maize research and breeding programmes. Drought tolerance is a complex quantitative trait resulting from the interaction of numerous physiological, morphological, biochemical, and genetic processes. Rather than relying on a single adaptive mechanism, drought-tolerant plants employ a combination of responses that enable them to maintain growth, reproduction, and survival under limited water availability. These responses include regulation of plant water status, maintenance of photosynthetic activity, efficient use of available water, modification of root architecture, osmotic adjustment, and protection against oxidative stress. The effectiveness of these adaptive mechanisms varies considerably among maize genotypes, creating opportunities to identify varieties with superior performance under water-limited condition.

One of the physiological characteristics associated with drought adaptation, water-use efficiency (WUE) has received considerable attention. WUE describes the relationship between plant productivity and water consumption and provides an important indicator of how efficiently plants utilise limited water resources. However, improving drought adaptation involves more than simply reducing water use, as excessive water conservation may also restrict photosynthesis and biomass accumulation. Consequently, understanding the physiological basis of WUE and its relationship with drought tolerance is essential for identifying maize varieties capable of maintaining productivity under increasingly water-limited environments. Significant genetic variation exists among maize varieties in their responses to drought stress. Previous studies have demonstrated substantial differences in physiological performance, water-use efficiency, and grain yield among maize genotypes exposed to contrasting water regimes (Ribaut et al., 2009; Cairns et al., 2013; Badu-Apraku et al., 2020). This variation provides an important resource for improving drought tolerance through the identification and selection of superior germplasm. Understanding how different maize varieties respond physiologically to water limitation is therefore fundamental for developing resilient cropping systems capable of sustaining production under changing

climatic conditions. In addition to maintaining grain yield, there is growing recognition that future maize varieties must also preserve grain nutritional quality under environmental stress. Maize constitutes a major dietary source of protein and essential nutrients for millions of people in developing countries, particularly where alternative protein sources are limited. Drought can alter nutrient uptake, assimilate partitioning, and grain development, potentially affecting protein concentration and overall nutritional quality. Consequently, evaluating nutritional responses alongside physiological adaptation provides a more comprehensive assessment of varietal performance under drought conditions and contributes to broader objectives relating to food and nutrition security.

Although substantial progress has been made in understanding the physiological and genetic mechanisms underlying drought tolerance, important knowledge gaps remain. Many previous studies have focused primarily on grain yield and agronomic performance, while comparatively fewer investigations have integrated physiological responses, water-use efficiency, and grain nutritional quality within the same experimental framework. Such an integrated approach is increasingly important because future climate-resilient maize varieties must combine drought adaptation with the ability to maintain nutritional value under water-limited conditions. Therefore, this chapter reviews the current understanding of physiological responses to drought stress, the role of water-use efficiency in drought adaptation, physiological indicators commonly used to evaluate drought tolerance, and the effects of drought on grain nutritional quality. The chapter concludes by identifying the existing knowledge gaps that underpin the objectives of the present study, which investigates variation in drought responses, water-use efficiency, and grain protein content among selected maize varieties grown under contrasting water regimes.

3.2 Physiological Responses of Maize to Drought Stress

Drought stress is one of the most important abiotic constraints affecting maize production worldwide, particularly in regions where crop production relies predominantly on rainfall. Water deficits influence virtually every aspect of plant growth and development, affecting physiological, biochemical, and reproductive processes that ultimately determine crop productivity. The magnitude of these effects depends on the timing, duration, and severity of water limitation, with drought occurring during the reproductive stage generally causing the greatest yield losses due to its adverse effects on pollination and grain development (Westgate and Boyer, 1986; Farooq et al., 2009).

One of the earliest physiological responses to declining soil moisture is a reduction in plant water status, leading to decreased leaf water potential and relative water content. These changes trigger a series of adaptive mechanisms aimed at conserving water and maintaining cellular function. Central to this response is the regulation of stomatal aperture. As soil moisture declines, stomata partially or completely close to reducing transpiration and minimize water loss. Although this response enhances short-term water conservation, it simultaneously restricts carbon dioxide diffusion into the leaf, thereby reducing photosynthetic carbon assimilation and limiting biomass production (Chaves et al., 2003; Tardieu, 2012). Consequently, prolonged stomatal closure often results in slower growth and reduced grain yield. Photosynthesis is particularly sensitive to drought stress. During mild water deficits, reductions in photosynthetic activity are primarily associated with stomatal limitations. However, under prolonged or severe drought, non-stomatal limitations become increasingly important. These include impaired chloroplast function, reduced activity of photosynthetic enzymes such as Rubisco, disruption of electron transport, and degradation of chlorophyll pigments (Flexas et al., 2004; Farooq et

al., 2009). Collectively, these changes reduce carbohydrate production, accelerate leaf senescence, and restrict assimilate availability for grain filling, ultimately decreasing productivity. Root systems play a fundamental role in drought adaptation because they determine the plant's ability to acquire water from the soil. Maize genotypes differ considerably in root architecture, with drought-tolerant varieties frequently exhibiting deeper rooting depth, greater root length density, and improved root proliferation in deeper soil horizons (Lynch, 2013). These characteristics enhance water acquisition during periods of limited rainfall and contribute to the maintenance of plant water status. Consequently, variation in root architecture represents an important physiological mechanism underlying genotypic differences in drought tolerance.

Plant hormonal signalling also contributes significantly to drought adaptation. Among the various phytohormones involved, abscisic acid (ABA) plays a central regulatory role. Water deficits stimulate ABA synthesis in both roots and leaves, initiating signaling pathways that promote stomatal closure, regulate osmotic adjustment, and activate stress-responsive genes involved in cellular protection (Zhang et al., 2006). While ABA-mediated responses improve survival under drought conditions by reducing water loss, prolonged activation of these pathways may also suppress vegetative growth and reproductive development, illustrating the balance between stress protection and productivity. At the cellular level, drought stress disrupts metabolic homeostasis and promotes the accumulation of reactive oxygen species (ROS), including superoxide radicals, hydrogen peroxide, and hydroxyl radicals. Excessive ROS production can damage proteins, lipids, nucleic acids, and cellular membranes, thereby impairing normal physiological processes (Farooq et al., 2009). To minimize oxidative damage, plants activate antioxidant defense systems comprising both enzymatic antioxidants, such as superoxide dismutase, catalase, and peroxidase, and non-enzymatic antioxidant compounds. Drought-tolerant genotypes generally possess more effective antioxidant defence mechanisms, enabling them to maintain cellular integrity and physiological function under prolonged water limitation.

Another important adaptive mechanism is osmotic adjustment, whereby plants accumulate compatible solutes including proline, soluble sugars, glycine betaine, and other osmolytes. These compounds help maintain cell turgor by lowering cellular osmotic potential, thereby allowing physiological processes to continue despite declining water availability (Blum, 2011). In addition to preserving water relations, osmolytes contribute to membrane stabilisation, enzyme protection, and maintenance of cellular metabolism. Differences in osmotic adjustment capacity among maize genotypes have therefore been recognised as important determinants of drought tolerance. The reproductive stage represents the most drought-sensitive phase of maize development. Water deficits during flowering frequently delay silk emergence, reduce pollen viability, impair fertilisation, and increase kernel abortion, resulting in substantial reductions in grain yield (Westgate and Boyer, 1986). These reproductive responses often have greater consequences for crop productivity than drought occurring during vegetative growth because successful pollination determines the number of kernels that ultimately develop into harvestable grain.

Numerous studies have demonstrated substantial variation among maize genotypes in their physiological responses to drought stress. Controlled-environment experiments and managed drought trials consistently show differences in the ability of genotypes to maintain water status, photosynthetic activity, reproductive development, and overall plant performance under limited water availability (Ribaut et al., 2009; Cairns et al., 2013; Badu-Apraku et al., 2020). This variation provides the biological foundation for identifying drought-adaptive traits and

selecting superior germplasm capable of sustaining productivity under increasingly variable climatic conditions. Understanding the physiological mechanisms underlying drought adaptation is essential for interpreting differences in varietal performance under contrasting water regimes. These responses not only influence plant survival and grain yield but also determine the efficiency with which available water is utilized. Consequently, water-use efficiency has emerged as one of the most widely studied indicators of drought adaptation and is discussed in the following section.

3.3 Water-Use Efficiency and Drought Adaptation

Water-use efficiency (WUE) is a fundamental physiological characteristic that describes the relationship between plant productivity and water consumption. As climate change intensifies the frequency and severity of drought events, improving WUE has become a major objective in crop improvement programmes because it offers the potential to sustain agricultural productivity while reducing dependence on increasingly limited water resources. In maize, WUE reflects the plant's ability to convert available water into biomass or grain yield and has therefore become an important indicator of drought adaptation, particularly in rain-fed agricultural systems where water availability is unpredictable (Blum, 2009).

The concept of WUE has evolved considerably over time and can be quantified at multiple biological scales depending on the objectives of a study. At the leaf level, intrinsic water-use efficiency (iWUE) is commonly defined as the ratio of the photosynthetic carbon assimilation rate (A) to stomatal conductance (gs), providing an indication of how efficiently carbon dioxide is assimilated relative to water lost through transpiration (Farquhar et al., 1989). At the whole-plant or crop level, WUE is generally expressed as the amount of biomass or grain yield produced per unit of water used through evapotranspiration. While these measurements describe different aspects of plant performance, both provide valuable information regarding the efficiency with which plants utilise available water under varying environmental conditions. Although higher WUE is often regarded as desirable under drought conditions, the relationship between WUE and drought tolerance is complex. Plants may achieve improved WUE through reduced transpiration, increased carbon assimilation, or a combination of both processes. However, excessive restriction of water loss through prolonged stomatal closure can simultaneously reduce carbon dioxide uptake, limiting photosynthesis, biomass accumulation, and ultimately grain yield. Consequently, drought adaptation should not be interpreted simply as maximizing WUE, but rather as maintaining an optimal balance between water conservation and productive growth (Blum, 2009; Blum, 2011).

Blum (2009) proposed the concept of Effective Use of Water (EUW), arguing that successful drought adaptation depends not only on improving water-use efficiency but also on maximising the productive use of available soil moisture throughout the growing season. According to this concept, plants capable of accessing greater soil water reserves through deeper or more efficient root systems may maintain higher photosynthetic activity and grain production despite experiencing lower instantaneous WUE. This perspective has significantly influenced modern approaches to drought research by emphasising overall crop productivity rather than focusing solely on water conservation. Genotypic variation in WUE has been widely reported in maize, reflecting differences in physiological regulation, root development, canopy architecture, and carbon assimilation efficiency. Numerous studies have demonstrated that drought-tolerant genotypes often exhibit superior regulation of gas exchange, improved maintenance of photosynthetic activity, and greater capacity to sustain biomass accumulation under water-limited conditions compared with drought-sensitive varieties (Condon et al., 2004; Cairns et al., 2013). Such variation provides valuable opportunities for identifying physiological traits

associated with superior drought adaptation and incorporating these characteristics into breeding programmes.

Several physiological and biochemical factors contribute to variation in WUE among maize genotypes. These include the regulation of stomatal conductance, maintenance of photosynthetic capacity, efficient partitioning of assimilates, root architecture, and the capacity to maintain cellular metabolism under declining water availability. Environmental conditions, including atmospheric vapour pressure deficit, temperature, solar radiation, and soil moisture availability, also exert considerable influence on WUE by affecting both transpiration and photosynthetic processes. Consequently, WUE should be considered as a dynamic trait resulting from interactions between plant genotype and environmental conditions rather than as a fixed physiological characteristic. Accurate assessment of WUE is essential for evaluating drought adaptation in both experimental and breeding programmes. Traditional approaches involve direct measurements of biomass production, grain yield, and water consumption under controlled irrigation regimes. More recently, physiological indicators such as carbon isotope discrimination ($\delta^{13}C$) have become valuable tools for estimating long-term intrinsic WUE. Carbon isotope discrimination reflects the ratio of the stable carbon isotopes ^{12}C and ^{13}C incorporated during photosynthesis and is closely associated with stomatal behaviour over the growing season (Farquhar et al., 1989). Because $\delta^{13}C$ integrates plant responses over time rather than representing a single measurement, it has become widely recognised as a reliable proxy for long-term water-use efficiency in many crop species, including maize.

Advances in high-throughput phenotyping have further expanded opportunities for evaluating WUE through the integration of physiological, imaging, and environmental measurements. Technologies including thermal imaging, multispectral sensors, chlorophyll fluorescence, automated lysimeters, and remote sensing platforms enable researchers to assess plant water status and physiological performance at much larger scales than traditional methods. These approaches facilitate rapid identification of drought-adaptive genotypes while improving the efficiency of breeding programmes aimed at developing climate-resilient maize varieties. Improving WUE has important implications beyond maintaining crop productivity. As freshwater resources become increasingly limited due to population growth, climate change, and competing demands from domestic and industrial sectors, crop varieties capable of producing higher yields with reduced water inputs will play a critical role in achieving sustainable agricultural production. For regions such as Sub-Saharan Africa, where maize cultivation is predominantly rain-fed, enhancing WUE represents an essential strategy for improving food security, increasing resilience to climatic variability, and supporting sustainable resource management.

Despite significant advances in understanding WUE, no single physiological measurement fully explains drought tolerance because adaptation results from the interaction of multiple complementary mechanisms. Consequently, researchers increasingly evaluate WUE alongside other physiological characteristics that provide additional insight into plant performance under drought conditions. These physiological indicators collectively improve the identification of drought-tolerant genotypes and are discussed in the following section.

3.4 Physiological Indicators of Drought Tolerance

The complex nature of drought tolerance necessitates the use of multiple physiological indicators to evaluate plant performance under water-limited conditions. Since drought affects numerous biological processes simultaneously, no single trait can adequately predict a genotype's capacity to withstand water deficits. Consequently, researchers employ a

combination of physiological measurements that collectively provide a comprehensive assessment of drought adaptation. These indicators facilitate the identification of superior genotypes, improve understanding of drought-response mechanisms, and support breeding programmes aimed at developing climate-resilient maize varieties (Blum, 2011; Cairns et al., 2013).

One of the most widely recognised indicators of drought tolerance in maize is the anthesis–silking interval (ASI), defined as the time difference between pollen shed (anthesis) and silk emergence. Under favourable environmental conditions, anthesis and silking occur almost simultaneously, ensuring efficient pollination and kernel development. However, drought stress frequently delays silk emergence without substantially affecting anthesis, resulting in an extended ASI. This delay reduces synchronisation between pollen availability and silk receptivity, increasing the likelihood of poor fertilisation, kernel abortion, and grain yield loss (Westgate and Boyer, 1986). Consequently, genotypes that maintain a short ASI under drought conditions are generally considered more drought tolerant and have been widely utilised in maize improvement programmes. Maintenance of leaf water status also provides valuable insight into drought adaptation. Relative water content (RWC) is commonly used to assess the hydration status of plant tissues and reflects the balance between water uptake and water loss. Plants capable of maintaining higher RWC during drought generally sustain greater metabolic activity, delay leaf senescence, and continue growth for longer periods than drought-sensitive varieties. Higher RWC therefore indicates superior water acquisition and conservation mechanisms and is frequently associated with improved drought resilience.

Stomatal conductance (gs) remains an important physiological indicator because it reflects the degree of stomatal regulation in response to declining water availability. Moderate reductions in stomatal conductance reduce transpiration and improve water conservation, whereas excessive or prolonged stomatal closure restricts carbon dioxide uptake and limits photosynthesis. Consequently, drought-tolerant maize varieties often exhibit more effective regulation of stomatal conductance, balancing water conservation with continued carbon assimilation. Measurements of stomatal conductance therefore provide valuable information regarding the physiological strategies employed by different genotypes under drought stress. Similarly, the ability to maintain photosynthetic capacity during water deficits is widely regarded as an important characteristic of drought-adapted plants. Drought-tolerant genotypes frequently sustain higher rates of carbon assimilation despite reduced soil moisture, allowing continued biomass production and grain filling. Measurements of net photosynthetic rate, chlorophyll fluorescence, and chlorophyll content are therefore commonly incorporated into drought evaluation studies because they provide direct evidence of the functional status of the photosynthetic apparatus. The stay-green phenotype has emerged as another valuable indicator of drought tolerance. Stay-green genotypes retain chlorophyll and photosynthetically active leaves for longer periods during grain filling, thereby extending the duration of assimilate production under drought conditions. Delayed leaf senescence enables continued photosynthesis during reproductive development, supporting kernel filling and reducing yield losses. Numerous studies have demonstrated positive associations between the stay-green trait and improved grain yield under terminal drought, making it an important selection criterion in maize breeding programmes.

Root characteristics also provide essential indicators of drought adaptation because water acquisition ultimately depends on root system architecture. Traits such as rooting depth, root length density, root biomass, and root distribution influence the plant's capacity to exploit soil moisture reserves. Deep and well-developed root systems enable plants to access water from deeper soil layers during prolonged dry periods, thereby supporting continued physiological

activity when surface soils become depleted. Although root traits are more difficult to measure than above-ground characteristics, advances in root phenotyping technologies have increased their application in drought research. Biomass accumulation and biomass partitioning provide additional information regarding plant performance under drought stress. Drought-tolerant genotypes generally maintain greater vegetative growth and allocate assimilates more efficiently to reproductive tissues despite reduced water availability. Consequently, measurements of shoot biomass, root biomass, harvest index, and dry matter accumulation are frequently used alongside physiological indicators to evaluate the overall impact of drought on plant productivity.

Water-use efficiency (WUE), discussed in the previous section, is also routinely incorporated into drought assessment because it reflects the effectiveness with which plants convert available water into biomass or grain yield. Measurements of intrinsic WUE, whole-plant WUE, and carbon isotope discrimination ($\delta^{13}C$) provide complementary information regarding long-term physiological performance under contrasting water regimes. When interpreted alongside other physiological indicators, WUE contributes to a more complete understanding of drought adaptation. Recent advances in plant phenotyping have substantially improved the assessment of drought tolerance by enabling simultaneous measurement of multiple physiological traits. High-throughput phenotyping platforms incorporating thermal imaging, multispectral imaging, chlorophyll fluorescence, hyperspectral sensors, and unmanned aerial vehicles (UAVs) allow rapid, non-destructive evaluation of large numbers of genotypes under field and controlled-environment conditions. These technologies improve the efficiency, precision, and scalability of drought screening while facilitating integration of physiological data into modern crop improvement programmes.

Because drought tolerance results from the coordinated interaction of multiple physiological processes, individual indicators should not be interpreted in isolation. Rather, integrating complementary measurements such as ASI, relative water content, stomatal conductance, photosynthetic performance, stay-green characteristics, root architecture, biomass production, and water-use efficiency provides a more robust assessment of drought adaptation. Such integrated physiological evaluation enhances the identification of resilient maize genotypes capable of maintaining productivity under increasingly variable climatic conditions.

The physiological indicators discussed in this section primarily evaluate plant responses associated with growth and productivity. However, drought also influences grain composition and nutritional value, which are increasingly recognised as critical components of crop performance. The following section therefore examines the effects of drought stress on maize nutritional quality, with particular emphasis on grain protein content and its implications for food and nutrition security.

3.5 Effects of Drought on Nutritional Quality

While the effects of drought stress on maize growth and grain yield have been extensively investigated, increasing attention has been directed towards understanding its influence on grain nutritional quality. This shift reflects growing concerns that climate change threatens not only crop productivity but also the nutritional value of staple foods. In many developing regions, particularly Sub-Saharan Africa, maize provides a substantial proportion of daily dietary energy and protein. Consequently, any drought-induced changes in grain composition may have important implications for food security, nutritional health, and sustainable agricultural production (Ranum et al., 2014).

Drought stress influences grain nutritional quality through its effects on nutrient uptake, carbon assimilation, assimilate partitioning, and grain development (Sehgal et al., 2018). Water limitation reduces soil water availability, restricting the transport of mineral nutrients to the root system while simultaneously suppressing photosynthetic activity and carbohydrate production. These physiological changes alter the balance between carbon and nitrogen metabolism during grain filling, thereby influencing the accumulation of storage compounds within the developing kernels. As a result, drought affects not only grain yield but also the nutritional composition of harvested maize. Among the nutritional components affected by drought, grain protein has received considerable research attention because of its importance in human nutrition. However, the effects of drought on grain protein concentration remain inconsistent across studies. Several researchers have reported increased grain protein concentration under moderate drought conditions, largely attributed to a concentration effect in which reduced starch deposition causes protein to represent a greater proportion of the final grain mass (Barutcular et al., 2016). In contrast, severe or prolonged drought may reduce nitrogen uptake, nitrate assimilation, and amino acid synthesis, thereby limit protein accumulation and reducing grain nutritional value (Farooq et al., 2009). These contrasting findings demonstrate that the nutritional consequences of drought depend not only on the severity and timing of water stress but also on environmental conditions and plant genotype.

Genetic variation further contributes to differences in nutritional responses among maize varieties. Badu-Apraku et al. (2015) reported substantial variation in grain nutritional traits among maize genotypes, suggesting that some varieties possess a greater capacity to maintain grain quality under drought conditions than others. Similarly, Ortiz-Monasterio et al. (2007) demonstrated that interactions between water availability, nitrogen supply, and genotype significantly influence grain nutrient composition. These studies highlight the importance of genotype-by-environment interactions in determining nutritional outcomes and emphasise that varietal differences should be considered when evaluating drought adaptation.

In addition to protein concentration, drought may affect the accumulation of essential micronutrients and bioactive compounds. Research on biofortified maize has shown that environmental stress can alter the concentration of provitamin A carotenoids and other nutritionally important compounds, although responses differ among genotypes and growing environments (Pixley et al., 2013). Such variation is particularly important in regions where maize constitutes a major dietary staple and deficiencies of vitamin A, iron, and zinc remain widespread. Maintaining nutritional quality under drought conditions therefore represents an important objective for future maize improvement programmes.

Despite increasing recognition of the relationship between drought stress and grain nutritional quality, much of the existing research has focused primarily on maintaining grain yield and improving agronomic performance. Comparatively fewer studies have investigated the relationships between physiological drought responses, water-use efficiency, and grain nutritional quality within the same experimental framework. This represents an important knowledge gap because physiological adaptation to drought may influence nutrient acquisition, assimilate allocation, and ultimately grain composition. Integrating physiological and nutritional assessments therefore provides a more comprehensive understanding of varietal performance than evaluating yield alone.

Accordingly, the present study investigates variation in grain protein content among selected maize varieties grown under contrasting water regimes while simultaneously examining physiological responses associated with drought adaptation. By combining nutritional and physiological assessments, this study aims to contribute to the development of maize varieties

capable of maintaining both productivity and nutritional quality under future climate scenarios.

3.6 Knowledge Gap and Chapter Objectives

Considerable progress has been made in understanding the physiological, agronomic, and genetic mechanisms underlying drought tolerance in maize. Previous studies have identified numerous physiological traits associated with drought adaptation, including stomatal regulation, water-use efficiency, root development, biomass retention, and anthesis-silking interval. Similarly, advances in molecular genetics and breeding have improved understanding of the complex genetic architecture controlling drought responses.

However, several important knowledge gaps remain. First, many drought-tolerance studies have focused primarily on grain yield and agronomic performance, with comparatively less attention given to the physiological mechanisms that contribute to adaptation under water-limited conditions. Second, although substantial genetic variation in drought responses has been reported, the extent to which physiological traits differ among maize varieties under contrasting water regimes remains incompletely understood. Third, relatively few studies have simultaneously evaluated physiological performance and grain nutritional quality, despite the importance of both traits for food security and climate resilience.

Furthermore, much of the existing literature has focused on identifying drought-tolerant genotypes through breeding programmes, while fewer studies have examined how physiological responses to drought are associated with nutritional outcomes. Understanding these relationships is particularly important in regions where maize serves as a major dietary staple and where climate change is expected to intensify water limitations.

Therefore, the present study was undertaken to investigate variation in drought responses among selected maize varieties grown under contrasting water regimes. The specific objectives were to:

1. Evaluate physiological responses of maize varieties under well-watered and drought-stressed conditions.
2. Assess variation in water-use efficiency and drought-adaptive traits among maize genotypes.
3. Determine the effects of drought stress on grain nutritional quality, with particular emphasis on protein content.

By integrating physiological and nutritional assessments, this study aims to provide a more comprehensive understanding of varietal adaptation to drought stress and contribute to ongoing efforts to develop resilient maize production systems under changing climatic conditions.

3.7. Materials & Methods

3.7.1 Plant Material

Two experiments were conducted to investigate genetic variation in maize water relations and responses to water limitation. The first experiment (Experiment 1) focused on artificial F2 populations developed to test the physiological effects of a quantitative trait locus (QTL) associated with photosystem II operating efficiency (ΦPSII), while the second experiment (Experiment 2) examined genetic variation in water-use-related traits using samples collected from a field-grown maize MAGIC population.

Full details of the development of the artificial F2 populations used in Experiment 1 are described in Heuermann, Caproni et al. (in press). Briefly, artificial F2 populations were generated using recombinant inbred lines (RILs) selected for contrasting haplotypes at a QTL located on chromosome 6 that was consistently associated with variation in ΦPSII in previous mapping analyses. For this QTL, a subset of RILs carrying haplotypes with positive effect on ΦPSII and a subset carrying haplotypes with a negative effect were identified. Lines from these two groups were randomly paired and crossed, producing F1 progeny that behave as an artificial F2 population at the targeted QTL position. As a result, the derived population segregates at the chromosome 6 locus in an approximate 1:2:1 ratio for the two parental haplotypes (+/+ , +/− and −/+ , and −/−), while the remainder of the genome is largely homogenised.

From this artificial F2 population, five founder-derived lines were selected for physiological analysis: SSA_200070, SSA_200072, SSA_200074, SSA_200076, and SSA_200080. Lines SSA_200070 and SSA_200072 carry the B96-derived haplotype at the chromosome 6 QTL, which has previously been associated with lower ΦPSII values. In contrast, lines SSA_200074, SSA_200076, and SSA_200080 carry the alternative haplotype at this locus, which is associated with higher ΦPSII. Based on this genetic contrast, plants carrying the non-B96 haplotype were expected to exhibit higher photochemical efficiency relative to B96-haplotype lines, providing a priori expectations for physiological responses under contrasting water availability. Plants were grown under controlled environmental conditions and subjected to two water treatments: a water-replete treatment and water-limited treatment. Water-replete plants were maintained under non-limiting soil moisture conditions, while water limitation was imposed by restricting irrigation to induce progressive soil drying.

The second experiment used plant material collected from a field trial of a maize multi-parent advanced generation intercross (MAGIC) population conducted in 2023. Full details of the MAGIC population and the field trial design are described in Ferguson et al. (2025). Briefly, the MAGIC population was developed from eight diverse maize inbred founder lines (A632, B73, B96, F7, H99, HP301, Mo17, and W153R) using a funnel breeding design, resulting in a large set of recombinant inbred lines with high allelic diversity and extensive recombination. The 2023 field trial was carried out at the National Institute of Agricultural Botany (NIAB), Cambridge, UK, under temperate field conditions. Recombinant inbred lines were grown in a replicated alpha-lattice experimental design, with individual genotypes arranged in multi-row plots to enable robust estimation of genotypic effects under field conditions. Standard agronomic management practices were applied throughout the growing season.

For the purposes of this study, randomly selected samples from this field-grown MAGIC population were used to quantify genetic variation in traits related to water use. Epidermal leaf impressions were collected to determine stomatal number, and dried leaf material was analysed for carbon isotope composition ($\delta^{13}C$) as an integrative measure of long-term water-use efficiency. In addition, previously published estimates of intrinsic water-use efficiency (iWUE) for the same plants were obtained from Xu et al. (2026) used to explore patterns of genetic variation and trait associations with non-integrated WUE. Together, these data enabled assessment of whether variation in stomatal anatomy and carbon isotope composition reflects underlying genetic variation in WUE within a genetically diverse maize population.

3.7.2 Growth conditions

For Experiment 1, artificial F2 lines were grown under controlled environmental conditions in “The Field” walk-in growth chamber within the Smart Technology Experimental Plant Suite.

Environmental conditions in the chamber were set to a day/night temperature regime of 22/20 °C, a 16 h photoperiod, photosynthetically active radiation of approximately 500 µmol m^{-2} s^{-1} at canopy height, and relative humidity maintained at ~60% (values indicative and to be adjusted as required).

Plants were established in 4 L pots containing a growth substrate composed of M3 compost, topsoil, and perlite mixed in a 1:1:0.5 ratio. To ensure adequate nutrient availability, 15 g of a continuous-release all-purpose fertiliser was incorporated per pot at planting. In addition, magnesium was supplied at a rate of one tablespoon of magnesium sulphate (Epsom salt) per pot. Following germination, seedlings were thinned to one plant per pot. Pots were arranged in a completely randomised design and repositioned periodically within the chamber to minimise positional effects related to light distribution and airflow.

All plants were maintained under well-watered conditions until growth stage V7, as defined by Robiul Alam et al. (2021). From this stage onwards, two irrigation regimes were imposed. Plants in the water-replete treatment received 2000mL of water per pot at two-day intervals, ensuring non-limiting soil moisture conditions. In contrast, plants in the water-limited treatment received 1200 mL of water per pot at two-day intervals, thereby limiting water availability relative to the control treatment. This approach enabled controlled comparison of physiological responses under contrasting levels of water supply.

For Experiment 2, plant material originated from a maize field trial conducted in 2023 under temperate conditions. As full details of the field trial design, management, and genetic material are provided elsewhere (see Plant Material; Ferguson et al., 2025), they are not repeated here. No experimental manipulation of water availability was imposed during the field trial.

3.7.3 Drought Stress Treatment

Maize seeds were sown on 4 June 2025 and maintained under uniform, well-watered conditions during the establishment phase. Seedlings were transplanted into 10 L pots on 15 June 2025 (11 days after sowing; DAS). Following transplantation, all plants received equal amounts of water to promote uniform establishment and growth.

Plants were subjected to water limitation through reduced irrigation on 21 July 2025 (47 DAS). The experiment consisted of two watering treatments: a well-watered control (Treatment 1) and a drought-stress treatment (Treatment 2). Control plants received 2000 mL of water per irrigation event, whereas drought-stressed plants received 1200 mL per irrigation event, representing a 40% reduction in irrigation volume. Irrigation was applied every two days between 12:00 and 13:00 h throughout the experimental period.

The drought treatment was maintained for seven days, from 21 July to 28 July 2025. Plants were harvested on 28 July 2025 (54 DAS) for physiological because plant height had increased substantially and exceeded the space available within the controlled growth environment. The stress period was sufficient to induce measurable differences in plant growth and physiological responses between treatments while ensuring that plants remained within the space constraints of the controlled growth environment.

3.7.3 Physiological Measurements

Physiological measurements were conducted to quantify variation in traits associated with water use, photosynthetic performance, and drought adaptation across the two experiments. These measurements were selected because drought tolerance is governed by multiple interacting physiological processes rather than a single characteristic. Consequently, evaluating complementary physiological traits provides a more comprehensive understanding of genotypic responses to water limitation than reliance on growth or yield measurements alone.

Experiment 1 focused on short-term physiological responses to controlled water-deficit treatments, including changes in soil moisture status, stomatal regulation, and photosynthetic performance. These measurements enabled direct assessment of plant responses immediately before and during drought imposition under controlled glasshouse conditions. Experiment 2 complemented these assessments by investigating structural and integrative physiological traits associated with long-term water-use efficiency, including stomatal number, carbon isotope composition ($\delta^{13}C$), and intrinsic water-use efficiency (iWUE). Together, these measurements captured both instantaneous and season-integrated responses to drought, providing complementary information on the mechanisms underlying variation in drought adaptation among maize genotypes.

3.7.4 Volumetric Water Content

Volumetric water content (VWC) was measured throughout Experiment 1 to monitor soil moisture dynamics and verify the effectiveness of the imposed irrigation treatments. Soil moisture monitoring was essential to ensure that plants assigned to the water-replete and water-limited treatments experienced consistent and distinct levels of water availability throughout the experimental period. By continuously assessing soil water status, VWC measurements provided quantitative confirmation that the irrigation treatments successfully generated the intended differences in soil moisture, thereby allowing physiological and morphological responses to be attributed to the experimental manipulation rather than uncontrolled variation in water availability.

Measurements were conducted using a WET-2 Soil Moisture Sensor (Delta-T Devices, Cambridge, UK), a portable instrument that estimates volumetric water content based on the dielectric properties of the soil. The sensor provides rapid, non-destructive measurements of soil moisture, making it well suited for repeated monitoring throughout the experiment without disturbing the root system or altering soil structure. Baseline VWC measurements were obtained immediately before the initiation of the irrigation treatments to confirm that all experimental pots started under comparable soil moisture conditions. Following treatment allocation, VWC was monitored regularly throughout the water treatment period to track changes in soil moisture resulting from the contrasting irrigation regimes. Monitoring was performed at approximately the same time of day during each sampling event to minimise variation associated with diurnal fluctuations in soil water content caused by evaporation and plant transpiration.

For each experimental pot, three technical measurements were taken by inserting the sensor at different positions within the soil while avoiding the immediate vicinity of the stem and the pot edges. This sampling strategy minimised the influence of localised heterogeneity in soil moisture distribution and provided a more representative estimate of the overall water content within each pot. The three measurements were subsequently averaged to generate a single VWC value for each pot at each sampling time, which was used for all subsequent statistical

analyses.Regular monitoring of VWC allowed verification that the water-replete treatment consistently maintained substantially higher soil moisture than the water-limited treatment throughout the experimental period. These measurements confirmed that the irrigation protocol successfully established and maintained contrasting water availability conditions, providing confidence that any observed differences in physiological performance, growth, or drought response among maize genotypes resulted from the imposed water treatments rather than inconsistencies in soil moisture management.

The VWC data were also used as an important quality-control measure throughout the experiment. Consistent separation between irrigation treatments demonstrated that treatment application remained stable over time, while repeated measurements enabled early detection of any unexpected deviations in soil moisture that could have compromised experimental integrity. Consequently, VWC measurements served both as verification of treatment implementation and as supporting evidence for interpreting subsequent physiological measurements, including chlorophyll fluorescence, stomatal conductance, gas exchange, and isotopic indicators of water-use efficiency.

3.7.5 Chlorophyll Fluorescence and Gas Exchange Measurements

Physiological measurements were carried out during Experiment 1 to evaluate how maize genotypes responded to contrasting water availability. These measurements focused on photosynthetic performance and stomatal behaviour, which are among the earliest physiological processes affected by drought stress. By assessing these traits before and during the water treatment period, it was possible to determine both the baseline physiological differences among genotypes and the extent to which these responses changed following the imposition of water deficit.

Measurements were obtained using a LI-COR LI-600 Porometer/Fluorometer, a portable instrument capable of simultaneously measuring chlorophyll fluorescence and stomatal conductance under field and glasshouse conditions. The instrument was selected because it provides rapid, non-destructive measurements, allowing the same plants to be monitored repeatedly throughout the experiment without causing damage to leaf tissues. To minimise variation associated with plant development, measurements were taken on fully expanded, healthy leaves of similar physiological age across all plants. Wherever possible, the same leaf position was used for repeated measurements to ensure consistency between sampling dates. Measurements were conducted both before the start of the irrigation treatments and throughout the water treatment period. Collecting data before treatment application provided a physiological baseline for each genotype, while repeated measurements during the experiment allowed changes associated with drought stress to be quantified over time. All measurements were carried out at approximately the same time of day to reduce the influence of diurnal variation on photosynthetic activity. Environmental factors such as light intensity, temperature and vapour pressure deficit can substantially influence chlorophyll fluorescence and stomatal conductance throughout the day. Standardising the timing of measurements therefore helped ensure that observed differences reflected treatment and genotypic effects rather than normal daily fluctuations in plant physiology.

The primary chlorophyll fluorescence parameter measured was the operating efficiency of Photosystem II (ΦPSII), which represents the proportion of absorbed light energy being used for photochemical processes during photosynthesis. This parameter provides an indication of the efficiency with which plants convert light energy into chemical energy under prevailing

environmental conditions. Since drought stress commonly reduces photosynthetic efficiency through both stomatal and non-stomatal limitations, ΦPSII was used to assess the extent to which different maize genotypes maintained photosynthetic performance under reduced water availability. Comparisons of ΦPSII between water-replete and water-limited plants enabled the identification of genotypic differences in the physiological response to drought. Genotypes that maintained relatively high ΦPSII values under water-limited conditions were considered to exhibit greater tolerance to water deficit, as sustained photochemical efficiency suggests that the photosynthetic apparatus remained functional despite reduced soil moisture. Conversely, larger declines in ΦPSII indicated increased sensitivity to drought stress and greater disruption of photosynthetic processes.

Stomatal conductance (gs) was measured simultaneously using the LI-600. Stomatal conductance quantifies the rate at which water vapour exits and carbon dioxide enters the leaf through the stomata, providing an important measure of plant water relations and gas exchange. Under drought conditions, stomata typically close to reduce water loss through transpiration. While this response conserves water, it also limits carbon dioxide uptake and may consequently reduce photosynthetic carbon assimilation. Measuring stomatal conductance alongside chlorophyll fluorescence therefore allowed the relationship between stomatal regulation and photosynthetic performance to be examined. Combining these two physiological measurements provided a more comprehensive understanding of plant responses to water deficit than either parameter alone. For example, reductions in ΦPSII accompanied by reduced stomatal conductance would suggest that decreased photosynthetic performance was associated with stomatal closure and restricted carbon dioxide availability. In contrast, reductions in ΦPSII without corresponding changes in stomatal conductance may indicate impairment of the photosynthetic machinery itself. Simultaneous measurement of these traits therefore helped distinguish between different physiological mechanisms underlying drought responses. These measurements were particularly important for evaluating maize genotypes differing at the chromosome 6 quantitative trait locus (QTL) previously associated with variation in ΦPSII. By comparing physiological responses under both water-replete and water-limited conditions, this study investigated whether allelic variation at the chromosome 6 QTL was associated with improved maintenance of photosynthetic efficiency and stomatal regulation during drought. The physiological data generated formed an important component of the subsequent statistical analyses used to identify genotypic variation in drought response and to evaluate the potential contribution of this genomic region to improved drought tolerance.

3.7.6 Stomatal Number

Stomatal number was determined in Experiment 2 to investigate variation in leaf epidermal characteristics among the maize genotypes and to assess whether differences in stomatal development were associated with variation in physiological responses to drought. Stomata are microscopic pores located on the leaf epidermis that regulate the exchange of carbon dioxide, oxygen and water vapour between the plant and the atmosphere. As they play a central role in both photosynthesis and transpiration, differences in stomatal number can influence plant water use, gas exchange and ultimately drought adaptation. Quantifying stomatal number therefore provided an additional anatomical trait that could be compared with the physiological measurements collected throughout the experiment.

Leaf samples were collected during the field season described previously. Fully expanded leaves were selected from plants at a comparable developmental stage to minimise variation resulting from differences in leaf age or maturity. Leaves showing signs of physical damage,

disease, or insect feeding were avoided to ensure that only healthy tissue was examined. To maintain consistency across all samples, impressions were taken from approximately the same region of each leaf, avoiding the midrib and the leaf margins where stomatal distribution may differ from the rest of the leaf surface. Leaf epidermal impressions were prepared using a dental resin impression material, which provides a reliable and highly detailed negative mould of the leaf surface. A thin layer of the resin was gently applied to the selected area of the leaf and allowed to set according to the manufacturer's instructions. Once hardened, the resin was carefully removed, producing a negative impression that accurately captured the surface features of the leaf epidermis, including the stomatal complexes.

To produce a positive replica suitable for microscopic examination, a thin layer of clear nail varnish was applied to the surface of the resin impression and left to dry completely. After drying, the nail varnish film was carefully peeled away using double-sided adhesive tape. This transparent film contained a detailed replica of the epidermal surface and was mounted onto a clean microscope slide for imaging. The nail varnish impression technique is widely used in plant anatomical studies because it is inexpensive, non-destructive and capable of producing high-quality epidermal replicas with minimal distortion. Microscopic examination was carried out using a Leica DM500 light microscope at 10× magnification. Images were captured from representative areas of the leaf epidermis while avoiding major veins and damaged tissue, as these regions may not accurately represent the overall stomatal distribution. Care was taken to ensure that image quality, focus and magnification remained consistent across all samples so that meaningful comparisons could be made between genotypes. Digital images were analysed using ImageJ (National Institutes of Health, USA), with the Cell Counter plugin used to manually identify and count individual stomata. Stomatal number was determined within a defined area of 1 mm^2 for each image, providing a standardised measure that enabled direct comparison among genotypes. Manual counting was preferred because it allowed each stomatal complex to be verified visually, reducing the likelihood of counting errors that can occur with fully automated image analysis, particularly where image contrast or epidermal features vary between samples.

Where multiple images were available from an individual leaf, counts were averaged to provide a representative estimate of stomatal number for each biological replicate. This approach helped minimise variation arising from local differences in stomatal distribution across the leaf surface and improved the reliability of the measurements. The resulting stomatal number data were used to examine anatomical variation among maize genotypes and to explore potential relationships with physiological traits measured during the study, including stomatal conductance (gs), photosystem II operating efficiency (ΦPSII), carbon isotope discrimination (δ13C), and plant responses to contrasting irrigation treatments. Integrating anatomical and physiological measurements allowed a more comprehensive assessment of the mechanisms underlying variation in water use and drought tolerance among genotypes.

3.7.7 Carbon Isotope Composition

Carbon isotope composition ($\delta^{13}C$) was measured in Experiment 2 to provide an integrated estimate of long-term intrinsic water-use efficiency (iWUE) among the maize genotypes grown under field conditions. Unlike instantaneous physiological measurements, such as stomatal conductance or chlorophyll fluorescence, which represent plant responses at the time of measurement, carbon isotope composition reflects the cumulative balance between carbon assimilation and water loss over an extended period of plant growth. As a result, $\delta^{13}C$ has become a widely used physiological indicator for investigating plant responses to water availability and identifying genotypic variation in water-use efficiency.

The principle underlying $\delta^{13}C$ analysis is based on the natural discrimination of plants against the heavier carbon isotope (^{13}C) during photosynthesis. During carbon fixation, the enzyme phosphoenolpyruvate carboxylase (PEPC) in C_4 plants, followed by Rubisco in bundle sheath cells, discriminates slightly against ^{13}C relative to the lighter isotope (^{12}C). The degree of discrimination is influenced by internal carbon dioxide concentration, which is itself affected by stomatal behaviour and photosynthetic activity. Consequently, variation in carbon isotope composition provides an integrated measure of the relationship between carbon uptake and water loss throughout plant development. In maize, although isotope discrimination is smaller than in C_3 species due to the C_4 photosynthetic pathway, $\delta^{13}C$ has nevertheless been shown to be a useful indicator of variation in intrinsic water-use efficiency and drought adaptation. Leaf tissue was collected from fully expanded, healthy leaves during the field experiment after plants had been exposed to the natural environmental conditions of the growing season. To minimise variation associated with developmental stage, samples were collected from comparable leaf positions across all genotypes. Any damaged, diseased or senescing tissue was avoided to ensure that isotope measurements reflected normal physiological functioning.

Following collection, leaf samples were oven-dried until a constant weight was achieved to remove all moisture while preserving the stable carbon isotope signature within the plant tissue. The dried material was subsequently ground into a fine, homogeneous powder using a laboratory grinding mill. Producing a uniform powder was essential to ensure that each subsample accurately represented the isotopic composition of the entire leaf sample and reduced variation associated with tissue heterogeneity. Approximately the required mass of finely ground material was weighed accurately into high-purity tin capsules using an analytical balance. Each capsule was carefully sealed to prevent sample loss or contamination during transport and combustion. The prepared samples were then packaged and submitted to the Goodwin Laboratory, University of Cambridge, for stable isotope analysis. Carbon isotope composition was determined using elemental analysis coupled with isotope ratio mass spectrometry (EA-IRMS). During analysis, each sample underwent complete combustion within the elemental analyser, converting all carbon present in the plant tissue into carbon dioxide (CO_2). The resulting gas was purified before being introduced into the isotope ratio mass spectrometer, where the relative abundances of the stable carbon isotopes (^{12}C and ^{13}C) were measured with high precision.

The $\delta^{13}C$ values obtained for each genotype were subsequently used to investigate genetic variation in long-term intrinsic water-use efficiency under field conditions. Because carbon isotope composition integrates physiological responses over several weeks of growth, it complements short-term physiological measurements such as stomatal conductance (gs) and photosystem II operating efficiency (ΦPSII). While gas exchange measurements provide a snapshot of plant function at a particular point in time, $\delta^{13}C$ reflects the cumulative effects of stomatal regulation and photosynthetic carbon assimilation throughout leaf development. Integrating $\delta^{13}C$ measurements with the physiological and anatomical traits measured in this study enabled a more comprehensive assessment of drought adaptation among the maize genotypes. Comparisons between $\delta^{13}C$, stomatal number, stomatal conductance and chlorophyll fluorescence helped determine whether genotypes that maintained greater photosynthetic performance under water-limited conditions also exhibited improved long-term water-use efficiency. This combined approach provided valuable insight into the physiological mechanisms underlying genotypic variation in drought response and contributed to the evaluation of traits associated with improved water-use efficiency in maize.

3.7.8 Intrinsic Water-Use Efficiency

Estimates of intrinsic water-use efficiency (iWUE) for the maize MAGIC population used in this study were obtained from the published dataset of Xu et al. (2026). As these measurements had already been generated as part of a previous investigation using the same mapping population, no additional gas exchange measurements were conducted during the present study. Instead, the published iWUE data were integrated with the anatomical, physiological and isotopic measurements collected here to investigate the relationships among different traits associated with drought adaptation and water-use efficiency.

Intrinsic water-use efficiency is widely recognised as an important physiological indicator of a plant's ability to balance carbon gain with water conservation. It describes the amount of carbon assimilated through photosynthesis relative to the degree of stomatal opening required for carbon dioxide uptake. Because stomata simultaneously regulate the uptake of atmospheric carbon dioxide and the loss of water through transpiration, iWUE provides valuable information on how efficiently plants utilise available water during photosynthesis. Genotypes with higher intrinsic water-use efficiency are generally considered to assimilate more carbon for a given level of stomatal conductance, making this trait particularly relevant for understanding plant performance under water-limited conditions.

In the study by Xu et al. (2026), intrinsic water-use efficiency was calculated as the ratio of the net photosynthetic CO_2 assimilation rate (A) to stomatal conductance (g_s). The gas exchange measurements used to calculate iWUE were obtained using a LI-COR LI-6400 Portable Photosynthesis System, one of the most widely used instruments for measuring leaf gas exchange in plant physiological research. The LI-6400 simultaneously measures carbon dioxide assimilation and transpiration while controlling environmental conditions within the leaf chamber, enabling accurate and repeatable estimates of photosynthetic performance. Measurements were conducted under standardised environmental conditions to minimise variation arising from external factors. Photosynthesis was measured under light-saturated conditions to ensure that carbon assimilation was not limited by light availability. The reference carbon dioxide concentration within the measurement chamber was maintained at 400 µmol mol^{-1}, representing ambient atmospheric CO_2 concentrations, while the block temperature was controlled at 25°C to provide a stable thermal environment during measurements. Relative humidity within the chamber was maintained at approximately 65%, thereby reducing variation in vapour pressure deficit that could otherwise influence stomatal behaviour.

Before recording each measurement, leaves were allowed sufficient time to equilibrate within the gas exchange chamber until photosynthetic rate and stomatal conductance had stabilised. This equilibration period ensured that the recorded values reflected steady-state physiological conditions rather than transient responses associated with placing the leaf inside the chamber. Following equilibration, measurements of net CO_2 assimilation rate and stomatal conductance were recorded according to established gas exchange protocols commonly used in plant physiological studies. The iWUE values generated by Xu et al. (2026) were incorporated into the present study to complement the physiological measurements collected during Experiments 1 and 2. Whereas stomatal conductance measured in this study provided an instantaneous assessment of stomatal regulation, and carbon isotope composition ($\delta^{13}C$) reflected integrated water-use efficiency over a longer period of growth, published iWUE estimates offered an additional measure of instantaneous physiological efficiency under controlled measurement conditions. Combining these datasets enabled water-use efficiency to be examined across multiple temporal scales. The published iWUE data were analysed alongside stomatal number, chlorophyll fluorescence (ΦPSII), stomatal conductance and carbon isotope composition to

investigate the relationships between leaf anatomy, photosynthetic performance and long-term water-use efficiency. In particular, the integration of these complementary traits allowed assessment of whether genotypes possessing greater stomatal densities or superior photosynthetic performance also exhibited higher intrinsic water-use efficiency. These comparisons provided a more comprehensive understanding of the physiological mechanisms contributing to drought adaptation within the maize MAGIC population and supported the identification of traits associated with improved water-use efficiency.

3.8 Results

3.8.1 Baseline Genetic Variation ΦPSII Prior to Water Treatments

To characterise baseline genetic variation in photochemical performance among artificial F2s, ΦPSII measurements collected up to 21 July, prior to the initiation of water treatments, were pooled across measurement dates. Mean ΦPSII values were plotted separately for each artificial F2 and grouped according to the treatment subsequently assigned (water-replete or water-limited), although all plants experienced identical watering conditions during this period (Figure 10).

Across all artificial F2s, ΦPSII values varied among genotypes, indicating the presence of baseline genetic variation in photochemical performance. No consistent separation was observed between plants assigned to the future water-replete and water-limited treatments, and trajectories for the two treatment groups largely overlapped across all artificial F2s.

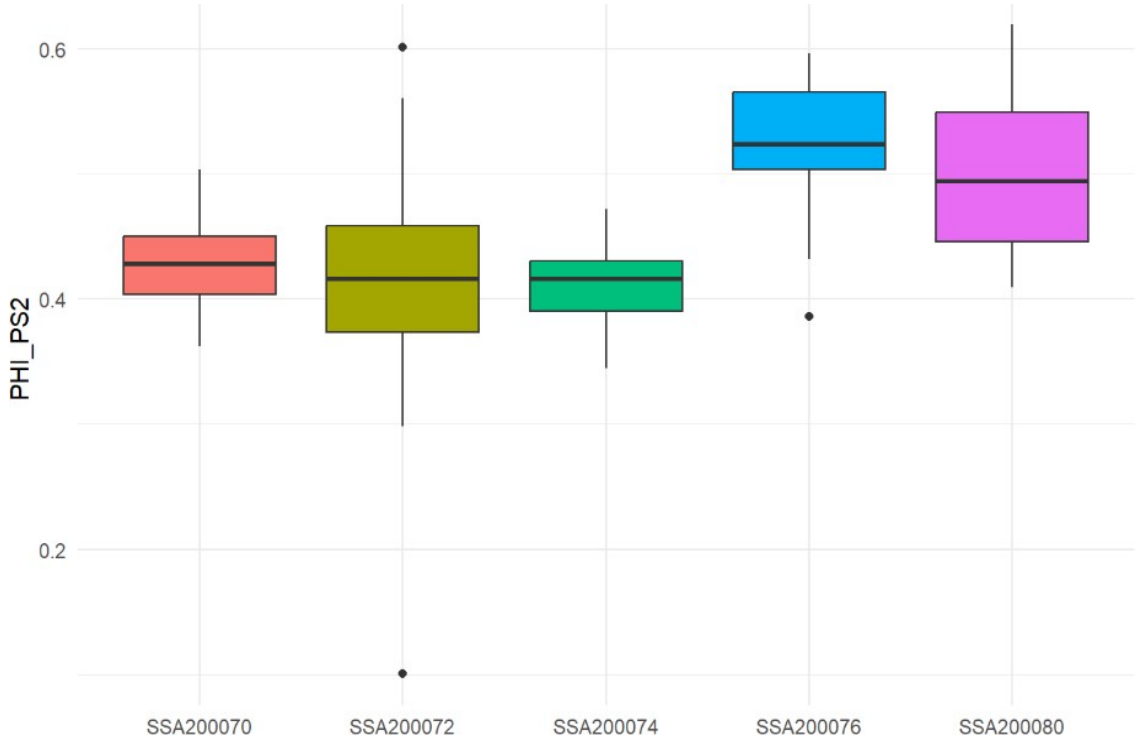


Figure 10. Baseline variation in photosystem II operating efficiency (ΦPSII) among maize artificial F2 lines prior to initiation of water treatments. ΦPSII was measured on the first day of physiological measurements, before the application of differential watering regimes. Data are pooled across plants later assigned to water-replete and water-limited treatments, as no differences in water availability were present at this time point. Boxes represent the interquartile range, with horizontal lines indicating median values; whiskers extend to 1.5× the interquartile range, and points represent outliers. –

Differences among artificial F2s were evident throughout the pre-treatment period. SSA200076 and SSA200080 consistently exhibited higher mean ΦPSII values, whereas SSA200070, SSA200072, and SSA200074 displayed comparatively lower mean values. Although some overlap in ΦPSII distributions occurred among artificial F2s, particularly among those with lower mean values, the overall ranking of genotypes remained relatively consistent across measurement dates.

These findings demonstrate the presence of baseline variation in photochemical efficiency among artificial F2 populations prior to the application of water treatments and confirm the absence of systematic differences between treatment groups before drought imposition.

3.8.2 Soil moisture dynamics and validation of water treatments

Volumetric water content (VWC) was monitored throughout Experiment 1 to assess changes in soil moisture over time and to verify that the irrigation treatments produced contrasting water availability. Mean VWC values for each treatment are presented in Figure 12 as a heatmap, illustrating the temporal changes in soil moisture throughout the experimental period. Before the irrigation treatments were imposed, VWC was similar across all experimental pots, indicating comparable initial soil moisture conditions. Following the introduction of differential watering, VWC declined progressively in the water-limited treatment, whereas soil moisture remained relatively stable in the water-replete treatment (Figure 11). The difference between treatments increased over time as the water-limited pots continued to dry while the water-replete pots received regular irrigation.

The largest differences in soil moisture were observed during the later stages of the experiment, reflecting the cumulative effects of restricted watering. These patterns indicate that the water-limited treatment experienced sustained soil drying, while the water-replete treatment maintained consistently favourable soil moisture conditions throughout the study. The observed separation in VWC between treatments confirms that the irrigation regimes successfully established contrasting soil moisture environments. This provided an appropriate experimental framework for evaluating the effects of water availability on physiological traits, including photosystem II operating efficiency (ΦPSII), stomatal conductance and other drought-related responses measured during the experiment.

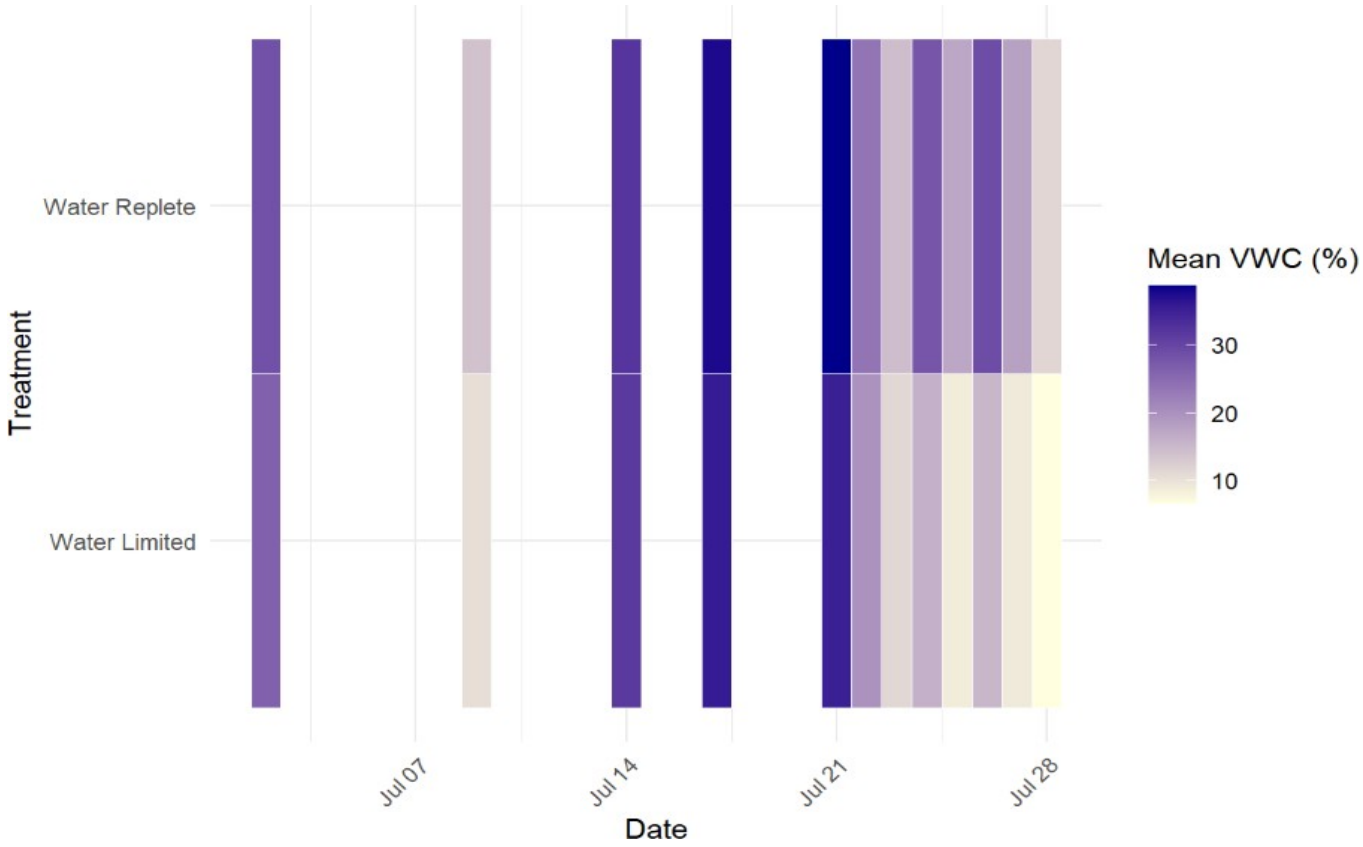


Figure 11. Heatmap showing mean volumetric water content (VWC, %) over time for water-replete and water-limited treatments during the experimental period. Mean VWC values are shown for each measurement date, averaged across artificial F2s within each treatment. Colour intensity represents relative soil moisture, with darker colours indicating higher VWC. The heatmap illustrates the temporal development of soil moisture conditions and the divergence between water-replete and water-limited treatments following initiation of differential watering.

3.8.3 Temporal dynamics of VWC across artificial F2s

Time-series plots of mean VWC for individual artificial F2s further illustrate treatment effects and temporal dynamics (Figure12). Across all artificial F2s, VWC declined following treatment initiation, with consistently lower values observed in the water-limited treatment compared to the water-replete treatment. While temporal fluctuations in VWC were evident, likely reflecting irrigation events and measurement timing, the relative difference between treatments was maintained across dates.

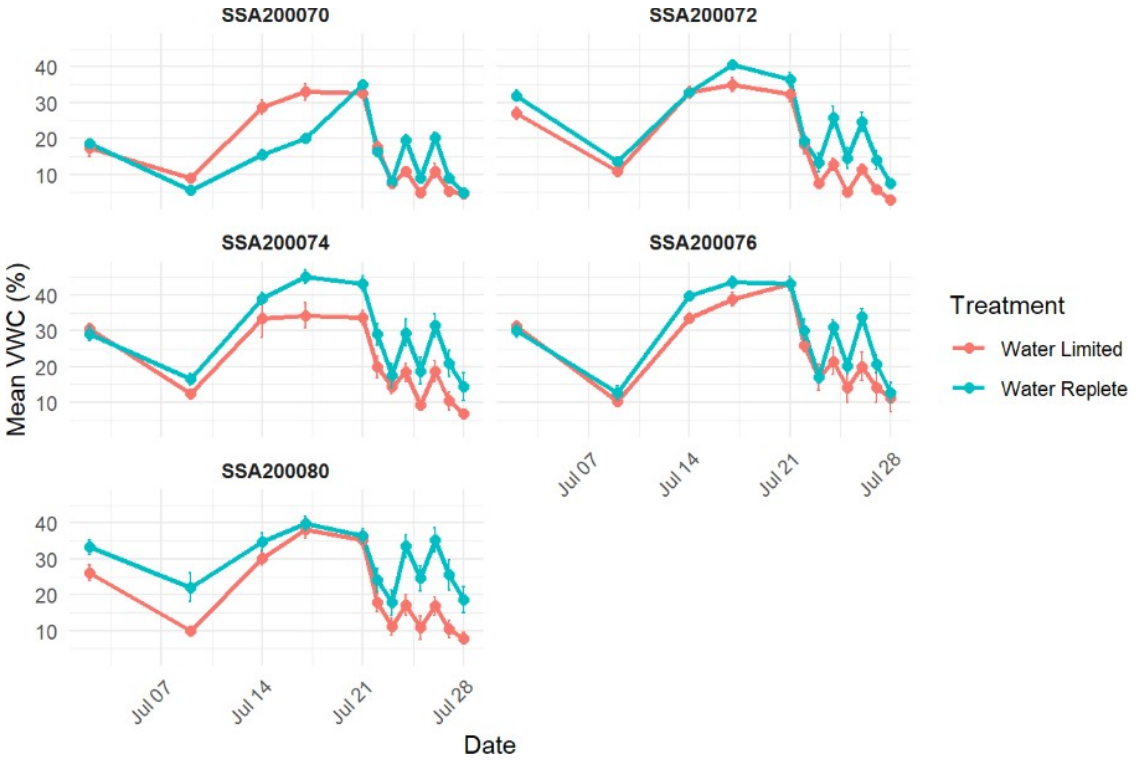


Figure 12. Time-series plots of mean volumetric water content (VWC, %) for each artificial F2 over the experimental period. Data are shown separately for water-replete and water-limited treatments. Points represent mean VWC values at each measurement date, with lines connecting successive time points to illustrate temporal trends. The figure shows the development of reduced soil moisture in the water-limited treatment relative to the water-replete control following initiation of differential watering, as well as temporal fluctuations in VWC across artificial F2s.

Statistical analysis confirmed these patterns (Table 2). Significant main effects of treatment and date were detected for VWC ($p < 0.001$), indicating that soil moisture differed between watering regimes and changed over time. A significant main effect of artificial F2 was also observed ($p < 0.001$). Significant treatment × date and variety × treatment interactions were detected, indicating that the magnitude of treatment effects varied over time and among artificial F2s. In contrast, the three-way interaction between variety, treatment, and date was not significant, suggesting that overall temporal treatment responses were broadly consistent across artificial F2s.

Table 2. Analysis of variance (ANOVA) for volumetric water content (VWC) showing the effects of artificial F2, water treatment, date, and their interactions.

Term	df	Sum of Squares	Mean Square	F value	P value
Artificial F2	4	31,380.605	7,845.151	43.623	<0.001
Treatment	1	16,363.647	16,363.647	90.990	<0.001
Date	1	25,543.356	25,543.356	142.034	<0.001
Artificial F2 × Treatment	4	5,783.831	1,445.958	8.040	<0.001

Artificial F2 × Date	4	2,345.032	586.258	3.260	0.011
Treatment × Date	1	3,052.179	3,052.179	16.972	<0.001
Artificial F2 × Treatment × Date	4	144.434	36.108	0.201	0.938

The ANOVA results for volumetric water content (VWC) show that soil moisture dynamics were driven primarily by irrigation regime and time rather than genotype. Both water treatment and date had highly significant effects on VWC ($p < 0.001$), with F values substantially exceeding those of genotypic terms, indicating that irrigation input and temporal progression were the dominant determinants of soil water content.

A significant main effect of artificial F2 was also detected ($p < 0.001$). In addition, significant treatment × date and artificial F2 × treatment interactions were observed, indicating that treatment effects varied over time and differed slightly among artificial F2s. However, the three-way interaction (artificial F2 × treatment × date) was not significant, suggesting that temporal patterns of soil moisture decline under drought were broadly consistent across genotypes.

The treatment × date interaction was particularly strong, indicating that divergence in VWC between water-replete and water-limited conditions increased as the experiment progressed.

3.8.4 Temporal trends in ΦPSII following initiation of water treatments

Temporal changes in photosystem II operating efficiency (ΦPSII) were examined following the initiation of water-replete and water-limited treatments. Mean ΦPSII values over time for each artificial F2 are shown in Figure 13, with measurements plotted separately for the two watering regimes.

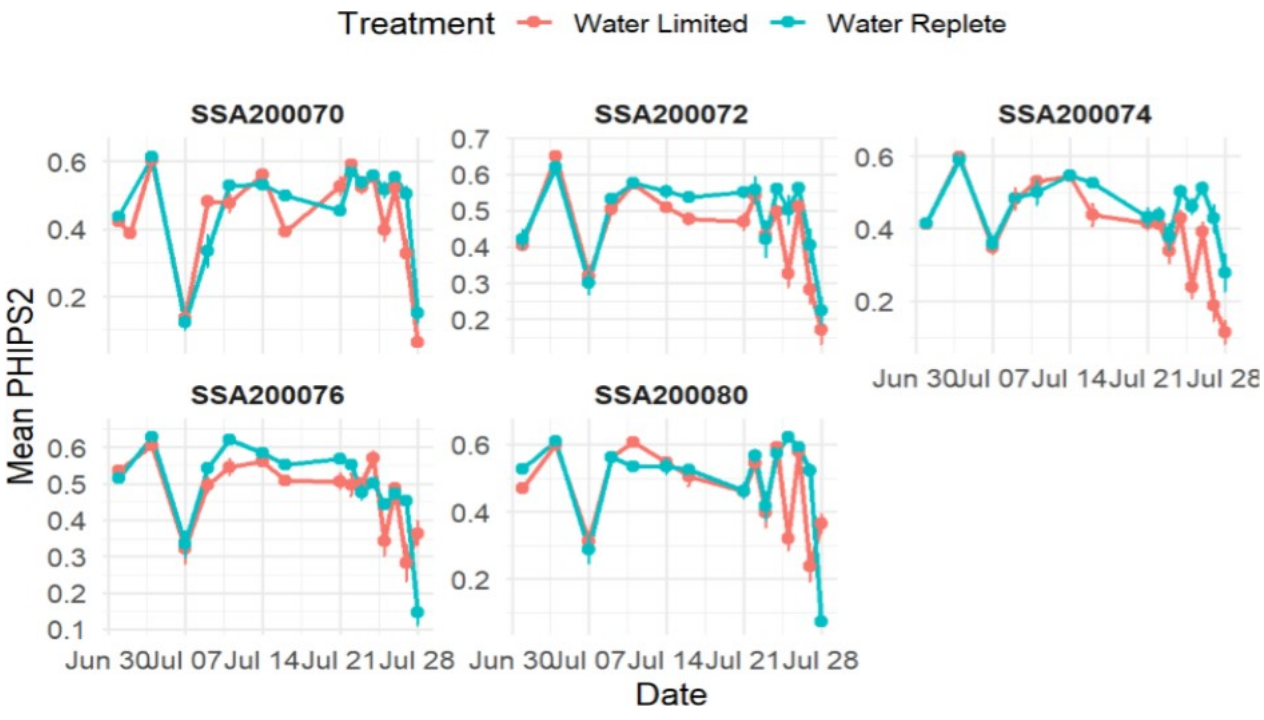


Figure 13. Time-series plots showing changes in photosystem II operating efficiency (ΦPSII) over the experimental period for each artificial F2 under water-replete and water-limited treatments. Mean ΦPSII values are shown for each measurement date, with points representing treatment means and lines connecting successive time points to illustrate temporal trends. Water treatments were initiated on 21 July, after which divergence between water-replete and water-limited plants became apparent in several artificial F2s, reflecting genotype-dependent temporal responses to reduced water availability.

Across all artificial F2s, ΦPSII exhibited clear temporal dynamics, with values declining towards the end of the experimental period (Figure 13). Following initiation of the water treatments, ΦPSII was generally lower in the water-limited treatment compared to the water-replete control, although the magnitude and timing of divergence varied among artificial F2s. In several artificial F2s (e.g. SSA200074 and SSA200080), reductions in ΦPSII under water limitation became increasingly pronounced later in the experiment, whereas other artificial F2s showed more modest or delayed responses.

Statistical analysis confirmed significant effects of artificial F2, treatment, and date on ΦPSII (Table X; $p < 0.001$), indicating that photochemical efficiency differed among genotypes, responded to water availability, and changed over time. Significant artificial F2 × treatment and artificial F2 × date interactions were also detected, suggesting that genotypes differed in both their sensitivity to water limitation and their temporal patterns of ΦPSII. In addition, a significant treatment × date interaction indicated that the effect of water limitation on ΦPSII varied over the course of the experiment.

Table 3. Analysis of variance (ANOVA) for photosystem II operating efficiency (ΦPSII) showing the effects of artificial F2, water treatment, date, and their interactions.

Term	df	Sum of Squares	Mean Square	F value	P value
Artificial F2	4	1.377	0.344	15.582	<0.001
Treatment	1	0.769	0.769	34.780	<0.001
Date	1	2.760	2.760	124.862	<0.001
Artificial F2 × Treatment	4	0.220	0.055	2.490	0.041
Artificial F2 × Date	4	0.870	0.218	9.845	<0.001
Treatment × Date	1	0.451	0.451	20.395	<0.001
Artificial F2 × Treatment × Date	4	0.352	0.088	3.980	0.003

3.8.5 Temporal trends in stomatal conductance following initiation of water treatments

Temporal changes in stomatal conductance (g_s) were monitored following the initiation of the water-replete and water-limited irrigation treatments to assess the physiological response of the maize genotypes to contrasting soil moisture conditions. Mean stomatal conductance values for each artificial F_2 genotype under both watering regimes are presented in Figure 14, with measurements shown across the experimental period.

Prior to the imposition of the water treatments, stomatal conductance was broadly similar

between plants assigned to the two irrigation regimes, indicating comparable physiological conditions before treatment began. Following treatment initiation, differences in stomatal conductance gradually became apparent as soil moisture declined in the water-limited treatment.

Across most artificial F_2 genotypes, plants maintained under water-replete conditions generally exhibited higher stomatal conductance than those exposed to water limitation. The reduction in g_s under water-limited conditions became more evident as the experiment progressed, although the magnitude of this response varied among genotypes. Some genotypes showed only a modest decline in stomatal conductance, whereas others exhibited a more pronounced reduction following the onset of water deficit.

Variation among genotypes was evident under both irrigation treatments, suggesting differences in stomatal regulation in response to soil water availability. While all genotypes were exposed to the same irrigation regimes, their temporal trajectories differed, indicating genetic variation in the physiological response to drought stress.

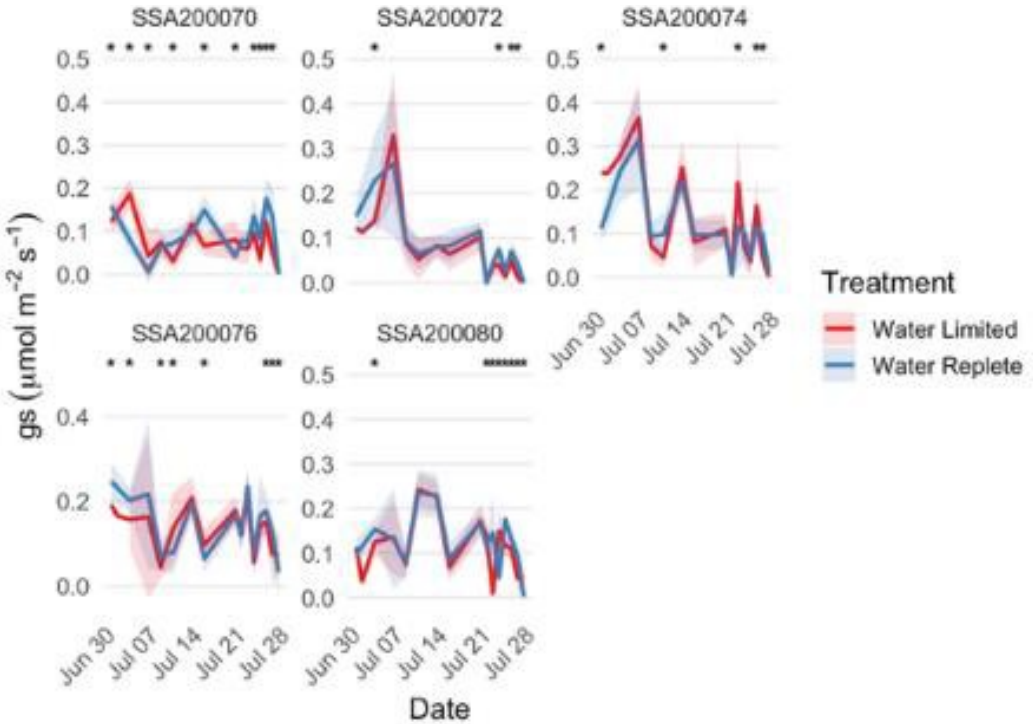


Figure 14. Time-series plots showing changes in stomatal conductance (g_s; µmol m^{-2} s^{-1}) over the experimental period for each artificial F2 under water-replete and water-limited treatments. Mean g_s values are shown for each measurement date, with lines connecting successive time points to illustrate temporal trends. Shaded areas represent variability around the mean. Water treatments were initiated on 21 July, after which water-limited plants generally exhibited lower g_s than water-replete controls, although the magnitude and consistency of treatment effects varied among artificial F2s and across dates.

Across all artificial F2s, g_s exhibited strong temporal variation over the course of the experiment (Figure 15. Following the initiation of water treatments, g_s was generally lower in the water-limited treatment compared to the water-replete control, although the magnitude and consistency of this response varied among artificial F2s. In some artificial F2s (e.g. SSA200076

and SSA200080), divergence between treatments was apparent across multiple time points, whereas in others the separation was more intermittent.

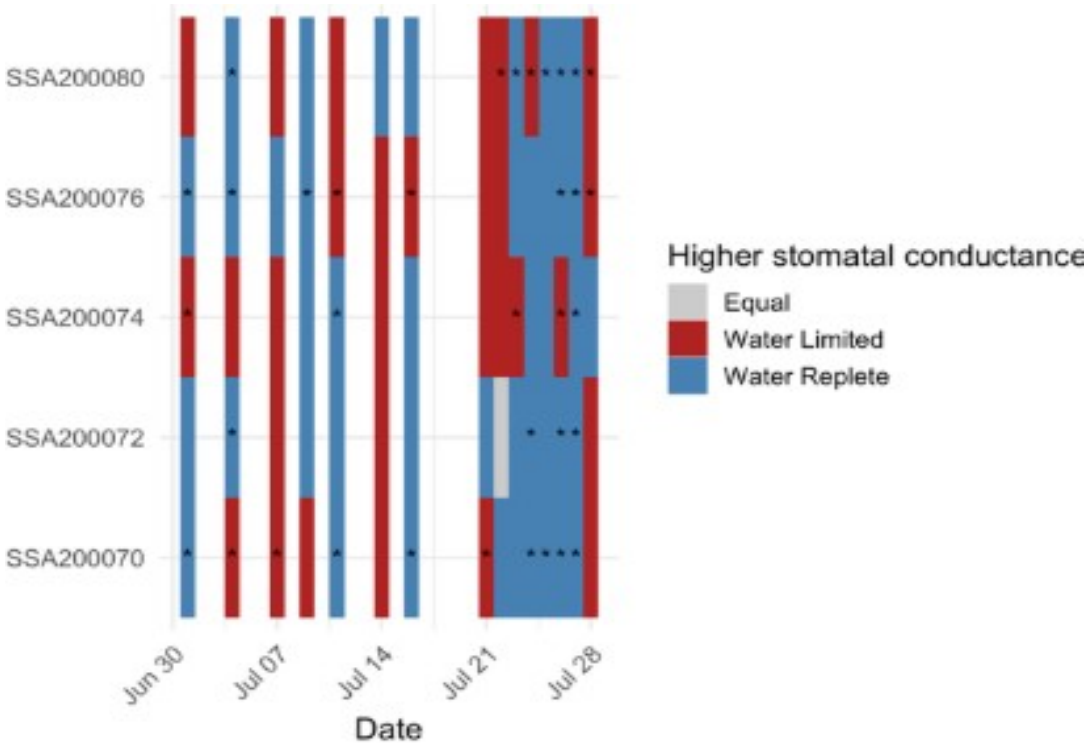


Figure 15. Heatmap showing the relative dominance of stomatal conductance (g_s) under water-replete and water-limited treatments across artificial F2s and measurement dates. For each artificial F2 and date, colours indicate whether mean g_s was higher under water-replete conditions, higher under water-limited conditions, or similar between treatments. The heatmap summarises genotype- and time-dependent differences in stomatal conductance responses to water availability over the course of the experiment.

The relative dominance of higher g_s values under water-replete or water-limited conditions across dates and artificial F2s is summarised in Figure 15. This categorical representation highlights that, while water-replete plants more frequently exhibited higher g_s values, periods of overlap or reversal occurred, particularly at earlier time points. These patterns indicate that treatment effects on stomatal conductance were dynamic and influenced by both genotype and time.

Statistical analysis supported these observations (Table 4). Significant main effects of artificial F2, treatment, and date were detected for g_s ($p < 0.05$), indicating that stomatal conductance differed among genotypes, responded to water availability, and changed over time. Significant artificial F2 × treatment and artificial F2 × date interactions were observed, demonstrating genotype-dependent sensitivity to water limitation and temporal variation in stomatal behaviour. In addition, a significant treatment × date interaction indicated that the effect of water limitation on g_s varied over the course of the experiment. The significant three-way interaction between artificial F2, treatment, and date further suggests that genotypes differed in how their stomatal responses to water limitation developed over time.

Table 4. Analysis of variance (ANOVA) for stomatal conductance (g_s) showing the effects of artificial F2, water treatment, date, and their interactions.

Term	df	Sum of Squares	Mean Square	F value	P value
Artificial F2	4	1.456	0.364	61.331	<0.001
Treatment	1	0.028	0.028	4.704	0.030
Date	1	2.713	2.713	457.023	<0.001
Artificial F2 × Treatment	4	0.072	0.018	3.042	0.016
Artificial F2 × Date	4	1.110	0.277	46.747	<0.001
Treatment × Date	1	0.034	0.034	5.659	0.017
Artificial F2 × Treatment × Date	4	0.098	0.025	4.140	0.002

3.8.6 Genetic variation in water-use-related traits in field-grown maize MAGIC lines

To characterise genetic variation in water-use-related traits under field conditions, stomatal number, carbon isotope composition ($\delta^{13}C$), and intrinsic water-use efficiency (iWUE) were analysed using data from the maize MAGIC population.

Substantial variation in stomatal number was observed among MAGIC lines (Figure 16). Stomatal counts spanned a broad and continuous range, indicating considerable genetic diversity in stomatal anatomy within the population. The distribution was continuous rather than discrete, consistent with stomatal number being a quantitatively inherited trait influenced by multiple genetic loci.

Carbon isotope composition ($\delta^{13}C$) also exhibited continuous variation across MAGIC lines (Figure 18). Values were distributed around a central mean, with both higher and lower $\delta^{13}C$ values present, indicating genetic variation in long-term intrinsic water-use efficiency under field conditions.

Intrinsic water-use efficiency (iWUE), obtained from previously published data, also varied substantially among MAGIC lines (Xu et al., 2026), with differences observed across the population consistent with a wide range of water-use strategies.

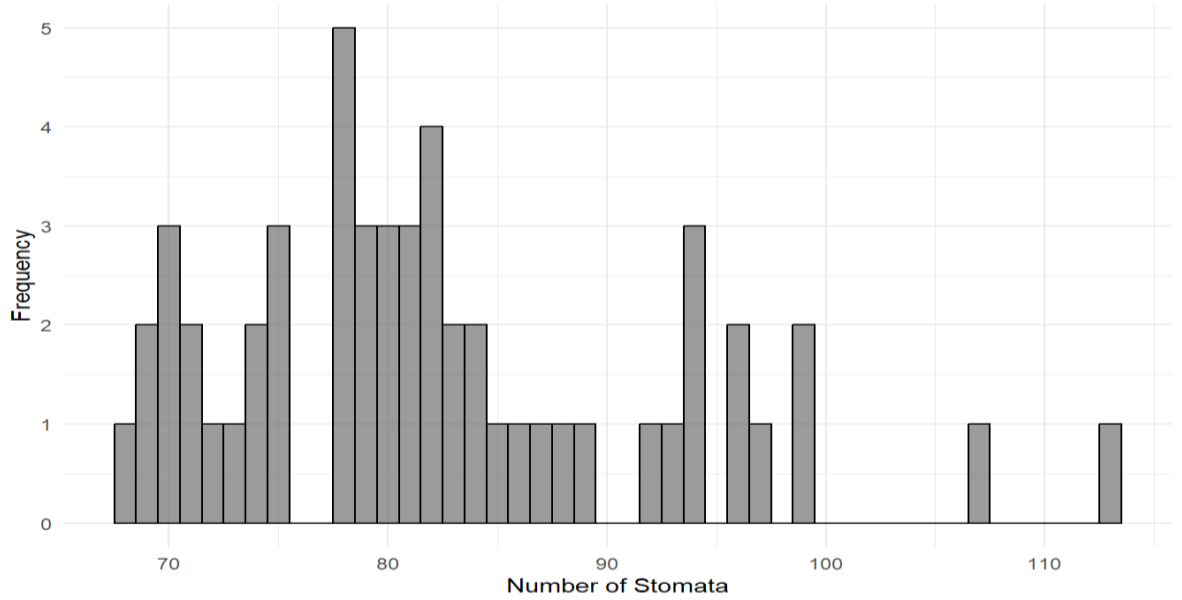


Figure 16. Variation in stomatal number among maize MAGIC lines under field conditions. Stomatal counts were measured on fully expanded leaves at the flowering stage. Data show a continuous distribution across the population, indicating polygenic control and substantial genetic diversity in stomatal density.

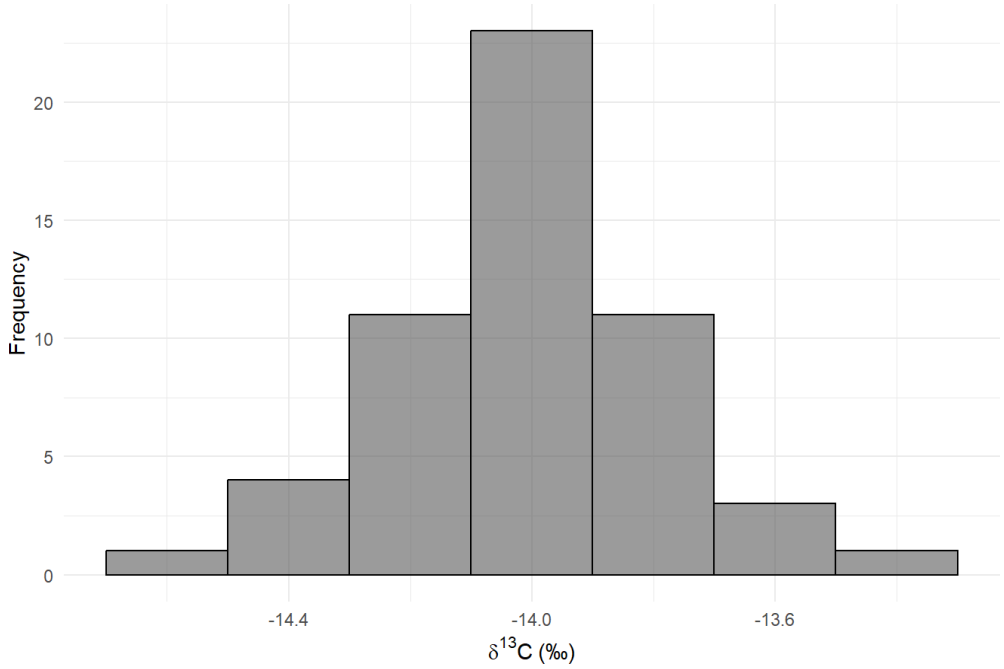


Figure 17. Distribution of $\delta^{13}C$ within the population. $\delta^{13}C$ values were measured on fully expanded leaves under field conditions. Data show a continuous distribution across the population, indicating substantial genetic variation in integrated water-use efficiency.

Relationships among stomatal number, $\delta^{13}C$, and intrinsic water-use efficiency were explored using correlation analysis (Figure 18). Stomatal number showed little to no correlation with $\delta^{13}C$, indicating that variation in stomatal anatomy was not directly associated with long-term water-use efficiency in this population. Similarly, stomatal number was weakly associated with intrinsic water-use efficiency. In contrast, $\delta^{13}C$ showed a modest negative correlation with

intrinsic water-use efficiency, consistent with theoretical expectations.

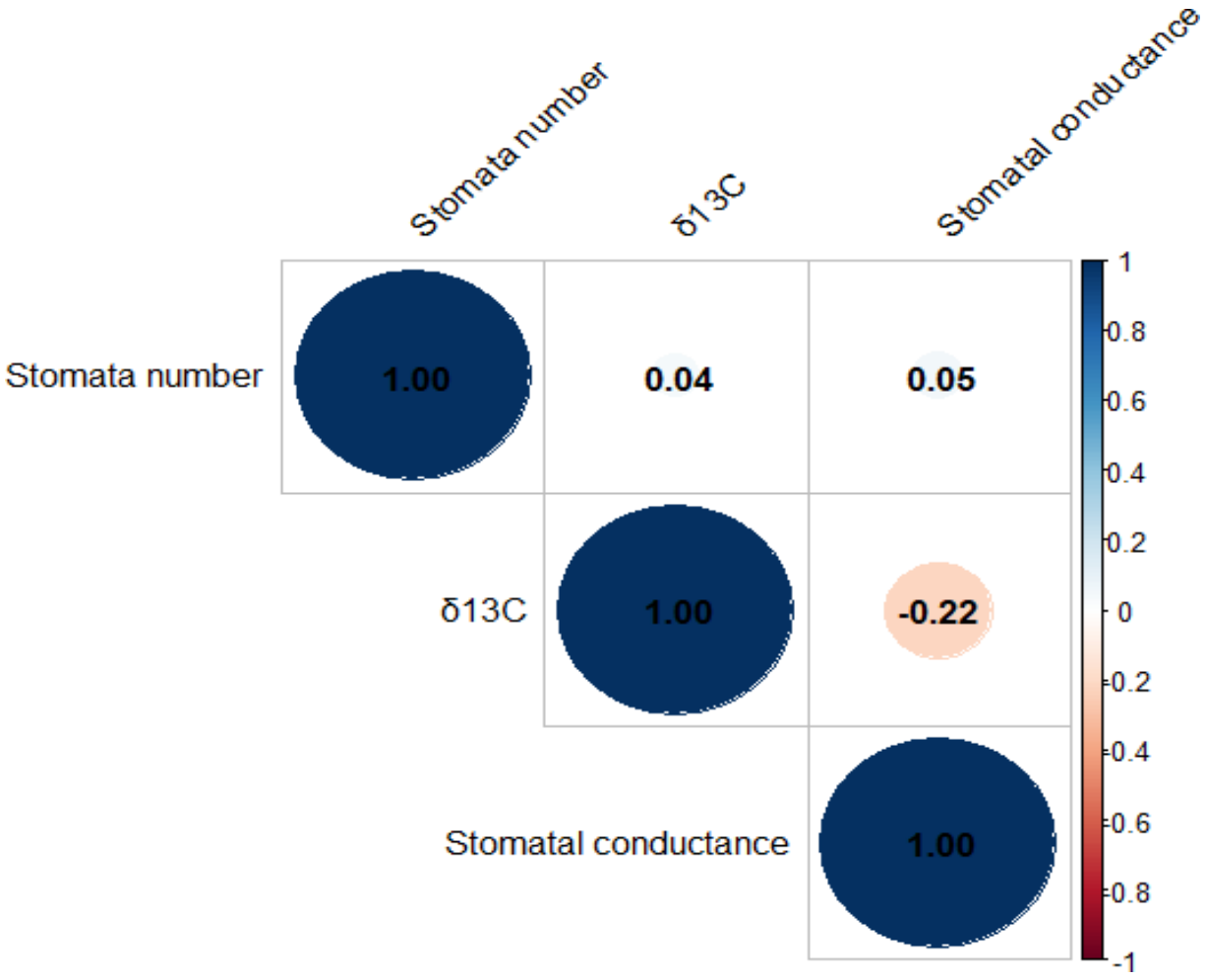


Figure 18. Relationships among stomata number, $\delta^{13}C$, and intrinsic water-use efficiency (iWUE) in field-grown maize MAGIC lines. Stomata number was not strongly correlated with $\delta^{13}C$ or iWUE, suggesting decoupling between stomatal anatomy and long-term water-use efficiency. In contrast, $\delta^{13}C$ showed a modest negative correlation with iWUE, aligning with expected physiological trade-offs. Stomatal conductance was measured under field conditions at midday; $\delta^{13}C$ was determined from mature leaf tissue.

3.9 Discussion

3.9.1 Soil Moisture Dynamics and Validation of Drought Treatments

The clear divergence in volumetric water content (VWC) between the water-replete and water-limited treatments confirmed the successful establishment of contrasting water environments during the experiment. Soil moisture declined progressively in the drought treatment following the withdrawal of irrigation, whereas moisture levels remained relatively stable in the well-watered treatment. This pattern demonstrates that the experimental design effectively imposed water limitation and provided a suitable framework for evaluating physiological responses to drought stress.

The strong effects of irrigation treatment and time on soil moisture were expected, as VWC directly reflects the balance between water inputs and losses through evaporation, drainage, and plant water uptake. Although significant genotype effects were detected, these were relatively small compared with the effects of irrigation treatment. Such differences may reflect variation in plant water use arising from differences in transpiration rates, canopy development, or root activity among genotypes. Importantly, the absence of a strong genotype × treatment interaction for soil moisture indicates that all genotypes experienced broadly similar drought conditions. Consequently, differences observed in physiological traits are likely to reflect genuine variation in drought response rather than differences in drought exposure. The ability to impose consistent drought conditions across genotypes is particularly important in studies of quantitative traits such as drought tolerance and water-use efficiency. Without uniform treatment conditions, it becomes difficult to distinguish true genetic variation from environmental artefacts. The soil moisture data therefore provide an important foundation for interpreting subsequent physiological responses observed during the experiment.

3.9.2 Genetic Variation in Baseline Photochemical Performance

Measurements collected prior to the initiation of drought treatments revealed clear differences in ΦPSII among artificial F_2 populations. Some genotypes consistently exhibited higher baseline photochemical efficiency than others, indicating the presence of inherent genetic variation in photosynthetic performance before the onset of water stress. The absence of systematic differences between plants allocated to future treatment groups further confirms that treatment assignment did not introduce bias into the experiment.

The observed ranking of artificial F_2 populations broadly agrees with the genetic architecture reported by Heuermann, Caproni et al. (in press), who identified a chromosome 6 quantitative trait locus associated with variation in ΦPSII. Artificial F_2 populations carrying haplotypes previously associated with enhanced photochemical efficiency generally exhibited higher baseline ΦPSII values in the present study. This correspondence provides confidence that the experimental material successfully captured variation at the target locus and supports the validity of the artificial F_2 approach for investigating genotype–phenotype relationships.

Although genotype rankings were generally consistent, overlap among some populations was evident. Such overlap is not unexpected because physiological traits are influenced by numerous genetic and environmental factors. Artificial F_2 populations retain residual segregation across the genome, and this background variation may influence the expression of photosynthetic traits. Furthermore, chlorophyll fluorescence measurements are inherently sensitive to subtle variation in leaf age, developmental stage, and microenvironmental conditions. These factors may contribute to within-genotype variability and reduce the apparent effect size of individual loci.

3.9.3 Temporal Responses of ΦPSII to Drought Stress

Following the imposition of drought, ΦPSII declined in water-limited plants relative to well-watered controls, indicating that water deficit affected photosynthetic performance. Reductions in ΦPSII under drought conditions are commonly interpreted as evidence of impaired photochemical efficiency resulting from limitations on electron transport, carbon assimilation, or photoprotective regulation (Flexas et al., 2004; Pinheiro and Chaves, 2010).

The temporal pattern observed in this study suggests that drought effects developed progressively rather than immediately following water withdrawal. This gradual response is

consistent with the physiological sequence typically observed during drought stress, whereby declining soil moisture first triggers stomatal closure and subsequently influences photosynthetic processes as stress intensifies. The maintenance of relatively high ΦPSII values during the early stages of drought may reflect the capacity of maize plants to buffer short-term reductions in water availability through physiological adjustment mechanisms.

Variation among artificial F_2 populations in the magnitude and timing of ΦPSII responses suggests genetic differences in the ability to maintain photochemical function under water deficit. Such variation is particularly relevant for breeding programmes because sustained photosynthetic performance under drought is often associated with improved productivity and stress resilience.

3.9.4 Stomatal Conductance and Regulation of Water Loss

Stomatal conductance exhibited strong temporal variation throughout the experiment and responded rapidly to changes in water availability. Plants exposed to drought generally showed lower stomatal conductance than those maintained under well-watered conditions, reflecting stomatal closure in response to declining soil moisture.

Stomatal regulation represents one of the earliest and most important plant responses to water deficit. By reducing stomatal aperture, plants limit transpirational water loss and help maintain plant water status. However, this response also restricts carbon dioxide uptake, creating a trade-off between water conservation and carbon assimilation (Blum, 2009). The observed reductions in stomatal conductance therefore likely contributed to the subsequent decline in photosynthetic performance under drought conditions.

Substantial variation among genotypes was evident, indicating that different artificial F_2 populations adopted contrasting strategies for regulating water loss. Some genotypes maintained relatively high stomatal conductance despite declining soil moisture, whereas others exhibited more rapid stomatal closure. These differences may reflect alternative drought-adaptation strategies, ranging from water-conserving behaviour to continued carbon acquisition under moderate stress. The presence of such variation highlights the complexity of drought tolerance and emphasises that multiple physiological pathways may contribute to improved performance under water-limited conditions.

3.9.5 Genetic Variation in Water-Use Efficiency

The combined patterns of variation in stomatal number, carbon isotope composition ($\delta^{13}C$), and intrinsic water-use efficiency demonstrate that water-use strategies in maize are inherently complex and cannot be explained by variation in a single trait. Substantial genetic diversity was observed for each trait, yet the relatively weak correlations among them suggest that different genotypes achieve similar levels of water-use efficiency through contrasting combinations of anatomical, physiological, and biochemical mechanisms.

Stomatal number represents a structural constraint on maximum gas exchange capacity, whereas $\delta^{13}C$ provides an integrated measure of long-term carbon assimilation relative to water loss. The weak association between these traits suggests that anatomical variation alone is insufficient to explain differences in water-use efficiency. Instead, factors such as stomatal behaviour, photosynthetic capacity, and environmental responsiveness are likely to play important roles in determining overall plant performance.

These findings are consistent with previous studies demonstrating that water-use efficiency is

a highly polygenic trait influenced by multiple interacting processes (Condon et al., 2004; Faralli et al., 2019). Consequently, breeding strategies based solely on a single physiological indicator may fail to capture the full complexity of drought adaptation.

3.9.6 Implications for Drought Tolerance and Breeding

The results of this study demonstrate the presence of substantial genetic variation for physiological traits associated with drought tolerance and water-use efficiency in maize. Differences among artificial F_2 populations were evident both before and after the imposition of drought stress, indicating that genetic factors influence photochemical performance, stomatal regulation, and water-use strategies.

Importantly, the findings suggest that drought tolerance cannot be attributed to a single trait. Instead, successful adaptation appears to arise from the interaction of multiple physiological mechanisms operating across different levels of biological organisation. Some genotypes maintained relatively high photochemical efficiency under drought, whereas others appeared to rely more strongly on conservative water-use strategies. This diversity of responses highlights the potential value of maintaining broad genetic variation within breeding programmes.

From a crop improvement perspective, the identification of genetic variation associated with water-use efficiency and drought response provides opportunities for developing maize varieties better adapted to increasingly variable climates. As drought events become more frequent and severe under climate change, understanding the physiological basis of stress resilience will be essential for sustaining maize productivity and food security. The results therefore contribute to ongoing effort at similar levels of water-use efficiency through contrasting combinations of anatomical, physiological, and biochemical mechanisms.

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4.0 Chapter Four: General Discussion and Conclusions

4.1 Introduction

This thesis investigated trait variation across social, physiological, and genetic traits of maize production. The research addressed two complementary questions. First, it examined how smallholder farmers in Kwara State, Nigeria, select maize varieties and how these preferences influence the cultivation of nutritionally important maize types. Second, it explored genetic variation for drought tolerance and water-use efficiency among maize genotypes under contrasting water regimes. Although these components were investigated separately, both address a common challenge facing maize improvement programmes: how to develop varieties that are not only productive and resilient under environmental stress but are also acceptable to farmers and capable of contributing to improved nutritional outcomes.

The findings demonstrate that maize improvement cannot be viewed solely as a genetic or physiological problem. Likewise, adoption cannot be explained entirely by farmer preferences. Successful maize varieties must satisfy multiple objectives simultaneously, including adaptation to drought stress, acceptable nutritional quality, marketability, and alignment with farmer priorities. This chapter integrates findings from both studies and considers their implications for breeding, policy, adoption, and future research.

4.2 Integrating Farmer Preferences, Nutritional Quality and Drought Resilience

One of the central findings of this thesis is that maize trait value depends on both biological performance and farmer perception. The farmer survey revealed that white and yellow maize varieties were both widely cultivated, with no significant difference in overall preference. This finding contrasts with the commonly held assumption that white maize is universally preferred in many parts of Sub-Saharan Africa and suggests that farmer preferences may be changing in response to evolving nutritional awareness, market opportunities, and local production conditions.

At the same time, nutritional analyses demonstrated variation in grain protein content among maize types, indicating that not all varieties provide equivalent nutritional benefits. This finding highlights a key challenge for maize improvement programmes. A variety that performs well nutritionally may not necessarily be the variety most widely cultivated, while a farmer-preferred variety may not always possess optimal nutritional characteristics. Consequently, nutritional improvement alone is unlikely to achieve meaningful impact unless improved varieties also satisfy farmer requirements.

The physiological and genetic studies provide an additional dimension to this challenge. Significant variation was observed among maize genotypes for traits associated with drought tolerance and water-use efficiency, including photochemical efficiency, stomatal conductance, and carbon isotope composition. These findings demonstrate that maize genotypes differ substantially in their responses to water limitation and that drought adaptation is controlled by multiple interacting mechanisms rather than a single trait.

When considered together, the results suggest that future maize varieties must combine three characteristics simultaneously: nutritional value, drought resilience, and farmer acceptability. Focusing on only one of these dimensions risks limiting the impact of breeding programmes. For example, a drought-tolerant genotype may fail if farmers perceive it as having poor grain quality or limited market demand, while a nutritionally enhanced variety may achieve little impact if it performs poorly under drought conditions.

The findings therefore support a more holistic approach to maize improvement in which farmer preferences are treated as an integral component of varietal development rather than an afterthought following genetic improvement.

4.3 Implications for Maize Breeding

The findings of this thesis have important implications for maize breeding programmes operating within Sub-Saharan Africa. Traditionally, breeding efforts have focused heavily on improving grain yield and adaptation to abiotic and biotic stresses. While these objectives remain important, the results of this study demonstrate that successful variety development requires a broader understanding of the factors influencing varietal performance and adoption. The farmer survey revealed that varietal selection is influenced by multiple considerations extending beyond productivity alone. Farmers considered characteristics such as grain colour, market demand, adaptability, and perceived quality when selecting maize varieties. Similar observations have been reported across several African countries where farmers often prioritise traits that directly influence household food security, marketability, and risk management (Asrat et al., 2010; Weltzien et al., 2019). These findings reinforce the argument that breeding programmes should not assume that improved agronomic performance alone will guarantee adoption.

An important finding from the survey was the absence of a strong preference for white maize over yellow maize. Earlier studies frequently reported a strong cultural preference for white maize in many African countries, often limiting the adoption of nutritionally enhanced yellow or orange maize varieties (De Groote et al., 2002; Stevens and Winter-Nelson, 2008). However, the present findings suggest that these preferences may be evolving. This shift could create opportunities for the wider adoption of biofortified maize varieties, particularly where awareness of nutritional benefits is increasing.

The physiological component of the study further demonstrated substantial genetic variation in drought-response traits, including ΦPSII, stomatal conductance, and indicators associated with water-use efficiency. The observed variation confirms previous reports that drought tolerance is a complex quantitative trait controlled by multiple interacting genetic and physiological mechanisms (Cairns et al., 2013; Tardieu, 2012). Consequently, breeding strategies focused on a single physiological trait are unlikely to capture the full complexity of drought adaptation.
The findings also support increasing interest in integrating physiological screening into breeding programmes. Traits associated with photosynthetic efficiency and water-use regulation may provide useful indicators of drought adaptation when combined with conventional agronomic selection criteria. Similar approaches have been advocated by Blum (2009), who argued that physiological understanding can improve the efficiency of breeding for water-limited environments.

Perhaps the most important implication of this thesis is that future maize breeding programmes should aim to combine nutritional quality, drought resilience, and farmer-preferred characteristics within the same variety. Historically, these objectives have often been pursued separately. However, the findings suggest that varieties capable of delivering meaningful impact under future climatic conditions will need to satisfy all three dimensions simultaneously. Breeding programmes that incorporate farmer participation during variety development may be particularly effective in achieving this balance (Ashby, 2009; Chiffoleau and Desclaux, 2006).

4.4 Implications for Agricultural Policy and Extension

The results also have important implications for agricultural policy and rural development initiatives. In many parts of Nigeria, efforts to improve agricultural productivity continue to focus primarily on increasing access to improved seed and agronomic inputs. While such interventions are important, the findings of this study suggest that successful adoption of improved maize varieties also depends on how well these varieties align with farmer priorities and local production systems.

The survey findings indicate that awareness of nutritional quality remains variable among farmers. Although nutritional improvement has become a major objective of many crop development programmes, information regarding the nutritional advantages of improved varieties does not always reach farming communities effectively. Similar concerns have been raised by Bouis and Saltzman (2017), who emphasised that the success of biofortification programmes depends not only on breeding progress but also on effective dissemination and awareness campaigns.

Agricultural extension services therefore have an important role to play in strengthening knowledge exchange between researchers, breeders, and farmers. Extension systems can help communicate information regarding improved varieties, drought adaptation strategies, and nutritional benefits while simultaneously providing breeders with valuable feedback regarding farmer priorities. Strengthening these feedback mechanisms may improve both the relevance and adoption of future maize varieties.

The findings also support continued investment in climate-resilient agriculture. Drought remains one of the most significant constraints affecting maize production across Sub-Saharan Africa (Lobell et al., 2014). The substantial variation observed among genotypes for drought-response traits suggests that considerable opportunities exist to improve resilience through targeted breeding and variety dissemination. Policies that support the development and distribution of drought-tolerant maize varieties could therefore contribute significantly to food security under increasingly variable climatic conditions.

4.5 Implications for Variety Adoption

A recurring theme throughout this thesis is that adoption is influenced by the interaction of biological, economic, and social factors. The findings demonstrate that varietal performance alone does not determine adoption. Rather, adoption reflects the extent to which a variety satisfies farmer objectives within a specific production environment.

This conclusion aligns with previous adoption studies showing that farmers evaluate technologies according to multiple criteria rather than a single performance indicator (Feder et al., 1985; Rogers, 2003). While breeders often prioritise yield and stress tolerance, farmers may place equal or greater emphasis on traits such as grain quality, market demand, maturity period, or storage characteristics.

The absence of significant differences between preferences for white and yellow maize may indicate increasing flexibility among farmers regarding varietal choice. Such flexibility could create favourable conditions for introducing nutritionally enhanced maize varieties, provided these varieties also meet expectations regarding productivity and marketability.

The findings therefore suggest that adoption strategies should move beyond simply distributing improved seed. Effective adoption programmes should incorporate farmer education,

demonstration trials, market development, and continuous engagement with local communities. Such approaches are more likely to generate sustained adoption than interventions focused solely on seed dissemination.

4.6 Study Limitations

Several limitations should be considered when interpreting the findings of this thesis. First, the farmer survey was conducted with a relatively small sample of twenty respondents from a single Local Government Area in Kwara State. Although the survey provided valuable insights into farmer preferences and perceptions, the findings cannot necessarily be generalised to all maize-growing regions of Nigeria. Farmer priorities may vary considerably across different agroecological, cultural, and socio-economic contexts. Consequently, the results should be interpreted as representative of the study area rather than the wider population of maize farmers.

Second, the survey employed a cross-sectional design, capturing farmer perceptions at a single point in time. Preferences and adoption decisions may change in response to market conditions, climatic variability, policy interventions, or exposure to new technologies. Longitudinal studies would provide a more comprehensive understanding of how these factors influence decision-making over time.

Third, survey responses were based on farmer self-reporting and may therefore be subject to recall bias, reporting bias, or social desirability bias. Respondents may not always accurately remember past experiences or may provide answers they perceive to be desirable or expected. While efforts were made to minimise these effects through direct interviews and clear explanation of survey questions, such biases are inherent limitations of questionnaire-based research.

Fourth, the physiology experiments were conducted under controlled environmental conditions. While controlled environments allow manipulation of water availability and facilitate the detection of physiological responses, they do not fully replicate the complexity of field conditions. Factors such as fluctuating temperatures, soil heterogeneity, pest and disease pressures, and genotype × environment interactions may influence drought responses under practical farming conditions. Consequently, caution should be exercised when extrapolating these findings to field environments.

Fifth, soil moisture content and pot weight were not monitored during the experimental period. As a result, the severity of water deficit experienced by the plants could not be quantified directly. The treatment should therefore be interpreted as a reduced-irrigation treatment rather than a precisely controlled drought-stress treatment. Future studies should incorporate direct measurements of soil moisture, field capacity, or pot weight to allow more accurate characterisation of plant water status and stress intensity.

Sixth, baseline differences between treatments were not statistically assessed before the reduced-irrigation treatment began. Consequently, some differences observed after treatment may reflect pre-existing variation among plants rather than responses to water limitation alone. In addition, physiological measurements may have been influenced by the time of day at which they were recorded, as photosynthesis, transpiration, and plant water relations are subject to diurnal variation. Future experiments should include baseline statistical comparisons, random allocation of plants to treatments after establishment, and standardised measurement times to minimise potential confounding effects.

Seventh, the reduced-irrigation treatment was applied for a relatively short period and at a single growth stage. Because maize sensitivity to water limitation varies throughout development, particularly during flowering and grain filling, the results may not fully capture responses that occur during other critical stages of growth. Additional experiments involving longer treatment periods and multiple developmental stages would provide a more comprehensive assessment of drought adaptation.

Eighth, nutritional quality assessment focused primarily on grain protein content. Although protein concentration is an important nutritional trait, maize nutritional quality also includes micronutrients, amino acid composition, provitamin A content, and grain-processing characteristics that were not evaluated in this study. A broader nutritional assessment would provide a more complete understanding of varietal differences and responses to water limitation.

Finally, while the artificial F_2 populations provided an effective framework for investigating genetic variation associated with drought tolerance, they represent only a subset of the genetic diversity available within maize germplasm. Additional studies involving larger and more diverse germplasm collections may reveal further sources of adaptive variation and improve the applicability of findings to breeding programmes.

4.7 Reflections on the Research

Looking back on the study, several aspects could have been strengthened. A larger and more geographically diverse farmer survey would have improved the robustness and representativeness of the social component of the research. Similarly, inclusion of additional nutritional measurements would have provided a more complete evaluation of maize quality.
Greater integration between the farmer survey and physiological experiments may also have strengthened the overall study. For example, directly evaluating the varieties preferred by farmers within the drought experiments could have provided a stronger link between social and physiological dimensions of maize improvement.

Despite these limitations, the study successfully achieved its objectives and generated insights that would not have been obtained through either social or physiological approaches alone. The integration of farmer perspectives with physiological and genetic analyses represents a significant strength of the research and contributes to a more holistic understanding of maize improvement.

4.8 Overall Conclusions

This thesis investigated trait variation across social, physiological, and genetic dimensions of maize production, with particular emphasis on farmer preferences, nutritional quality, drought tolerance, and water-use efficiency. The study was motivated by the recognition that future maize improvement efforts must address multiple challenges simultaneously, including climate change, food and nutrition security, and the need for widespread adoption of improved varieties by smallholder farmers. By integrating farmer survey data with physiological and genetic analyses, the research provides a broader understanding of the factors influencing maize performance and utilisation within smallholder farming systems.

The first objective of the study was to identify the key traits influencing smallholder farmer preferences for maize type and nutritional quality. The findings demonstrated that farmer decision-making is influenced by multiple and interacting factors rather than by a single

characteristic. Farmers considered attributes such as grain colour, market demand, adaptation to local conditions, and perceived quality when selecting maize varieties. Although white maize remained widely cultivated, no significant difference in preference was observed between white and yellow maize, suggesting that varietal preferences may be changing. This finding is particularly important because it indicates potential opportunities for the adoption of nutritionally enhanced maize varieties where appropriate awareness and dissemination strategies are implemented.

The second objective was to evaluate the nutritional quality of commonly grown maize varieties. The results revealed variation in grain protein content among maize types, demonstrating that nutritional quality differs across varieties cultivated within the study area. These findings reinforce the importance of considering nutritional traits within maize improvement programmes. However, the study also demonstrated that nutritional superiority alone is unlikely to guarantee adoption. Farmer preferences and production realities continue to play a central role in determining which varieties are cultivated and maintained within local farming systems.

The third objective was to assess the impact of drought stress on key physiological traits associated with maize performance. The controlled-environment experiments confirmed that drought stress significantly influenced soil moisture dynamics, photochemical efficiency, and stomatal conductance. Water limitation reduced physiological performance and revealed substantial variation among genotypes in their responses to drought. These findings highlight the importance of drought as a major constraint on maize production and emphasise the need for continued investment in the development of climate-resilient varieties.

The fourth objective was to explore genetic variation for drought stress response in relation to water-use efficiency and nutritional quality. Significant variation was observed among maize genotypes for traits associated with drought adaptation, including ΦPSII, stomatal conductance, and indicators of water-use efficiency. The results demonstrated that drought tolerance is a complex trait controlled by multiple interacting physiological mechanisms rather than a single genetic factor. Furthermore, the study showed that different genotypes may achieve similar levels of adaptation through contrasting physiological strategies. This finding highlights the value of maintaining broad genetic diversity within breeding programmes and supports the use of integrated physiological and genetic approaches in crop improvement.

Taken together, the findings of this thesis demonstrate that successful maize improvement requires the integration of social, physiological, and genetic perspectives. Farmer preferences determine whether improved varieties are adopted, physiological traits influence performance under environmental stress, and genetic variation provides the foundation upon which breeding progress depends. Focusing exclusively on any one of these dimensions risks limiting the effectiveness of improvement programmes. Instead, future maize varieties should be developed with the objective of combining drought resilience, improved nutritional quality, and traits that align with farmer needs and market demands.

The study also contributes to broader discussions surrounding food security and agricultural sustainability in Sub-Saharan Africa. As climate change increases the frequency and severity of drought events, maintaining maize productivity will become increasingly challenging. At the same time, improving the nutritional quality of staple crops remains essential for addressing hidden hunger and supporting human health. The findings presented here suggest that these goals are most likely to be achieved through interdisciplinary approaches that integrate

biological research with an understanding of farmer behaviour and decision-making.

In conclusion, this thesis demonstrates that variation in maize performance extends beyond physiological and genetic characteristics to include the social factors that influence varietal adoption and long-term utilisation. By linking farmer preferences with nutritional quality and drought-response traits, the research provides a more holistic understanding of maize improvement and highlights the importance of developing varieties that are not only productive and resilient but also acceptable and beneficial to the farming communities that depend upon them. Such an integrated approach will be critical for supporting sustainable maize production and strengthening food and nutrition security in Sub-Saharan Africa under future climatic conditions.

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Appendix

The following questions were asked during the survey:

1. Do you grow different maize varieties? (Yes / No)
2. If yes, what different maize varieties do you grow? (List all varieties)
3. How do you obtain the seeds for the different maize varieties you grow?
    a. Saved seeds from previous harvest
    b. Purchased from a seed dealer
    c. Obtained from a government agricultural programme
4. Do you sell your maize? (Yes / No)
5. How important is market demand for specific maize varieties in your decision to adopt different maize varieties?
    a. Very important
    b. Somewhat important
    c. Not important
6. In your opinion, which maize varieties are in high demand in the market?
7. Are you aware of the nutritional benefits of different maize varieties? (Yes / No)
8. If yes, how important is the nutritional value of maize varieties in your decision to grow them?
    a. Very important
    b. Somewhat important
    c. Not important
9. What other factors influence your decision to grow different maize varieties (e.g., pest and disease resistance, drought tolerance, yield potential)?
10. Have you participated in any government or non-governmental organisation programme aimed at improving crop biodiversity or maize production? (Yes / No)
11. What challenges do you face when growing different maize varieties (e.g., lack of resources, lack of knowledge, lack of support)?
12. Do you grow maize under a traditional farming system, an organic farming system, or both?
13. Are you familiar with or have you used any traditional or indigenous methods of maize cultivation (e.g., intercropping, crop rotation)? (Yes / No)
14. Are you willing to adopt new maize varieties if they are proven to be more nutritious, higher yielding, or more resistant to pests and diseases? (Yes / No)
15. Do you think increasing crop biodiversity in maize cultivation can improve food security in your community? (Yes / No)
16. What kind of support or resources would you need to improve maize cultivation and increase crop biodiversity?

- Training and education on new techniques and varieties
- Financial support for purchasing seed or inputs
- Support from government or non-governmental organisations

17. How do you plan to use the maize you produce?

- Household consumption
- Sale in the local market

- Sale in the national market
- Other purposes (e.g., animal feed, seed for the next planting season)

RC: Kw7413

M.B.S GOLDEN LINKS CONCEPT

Dear Sir or Madam,

It is with great pride that we inform you that one of our employees, Mrs Arikewusola Ganiyat, has been accepted into the Masters by Dissertation (MSD) program in the Department of Life science (Environmental Biology) at the University of Essex.

As part of her MSD program, Mrs Arikewusola Ganiyat will be conducting research on enhancing crop biodiversity in maize cultivation for improved food security in Ilorin South Local Government Area, Kwara State, Nigeria.

The research project is a one-year program, and Mrs Arikewusola Ganiyat will be using various methodologies, including interviews with farmers, field surveys and statistical analysis of crop data to achieve the following objectives.

1. Investigating the nutritional composition of diverse maize varieties to identify high-nutrient and biofortified varieties for improving dietary diversity and addressing malnutrition.
2. Examining the socio-economic factors influencing the adoption of diverse maize varieties by smallholder farmers including access to seeds, market demand and farmers knowledge.
3. Assessing the impact of climate change in maize genetic resources and identifying strategies for conserving and utilizing crop biodiversity to enhance food security resilience.
4. Documenting traditional knowledge and indigenous maize landraces to understand their role in preserving crop biodiversity and contributing to food security resilience.

We believe that the findings of this research will not only contribute to the advancement of agriculture and food security in Ilorin South Local Government Area, but also provide insights and strategies for addressing broader issues of malnutrition, climate change and food security resilience.

As Mrs Arikewusola Ganiyat's employer, we are fully supportive of her participation in this important project.

Mrs Arikewusola Ganiyat's research aligns with our company's commitment to promoting sustainable agriculture, environmental conservation and food security. We are proud to have an employee of Mrs Arikewusola Ganiyat's caliber and commitment on our team, we look forward to the valuable contribution that this research will make to our understanding of crop biodiversity, maize cultivation and food security.

Yours sincerely,

M.B.S GOLDEN LINK CONCEPT Sign: Date:

Jimoh Sulaimon

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