WATER USE EFFICIENCY AND SOIL CARBON SEQUESTRATION OF SELECTED INDIGENOUS AND MODERN CROP CULTIVARS FOR SUSTAINABLE AGRICULTURE INTENSIFICATION AND CLIMATE CHANGE MITIGATION

Report to the
WATER RESEARCH COMMISSION

by

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EXECUTIVE SUMMARY

BACKGROUND

General context and research problem: the need for climate-smart crops

Major cereal crops such as wheat and sorghum are significant contributors to global food security and economies but their high water demand for growth, development, and productivity is competing for the scarce water resources. In the context of water insecurity in the face of climate variability and climate change, improving water use efficiency (WUE) in cereals is more urgent than ever through synergistic actions by the target growers, breeders, and agronomists. Crops with high biomass production have the potential of capturing carbon (C) from the atmosphere and transfer it to their tissues and ultimately to soils. Therefore, these crops can play a key role in fighting climate change due to the potential of carbon sequestration in soils. Farmers in sub-Sahara African (SSA) face not only water scarcity but also marginal soil fertility, with soils having lost from 30 to 50% of their carbon stocks. Carbon is the main constituent of soil organic matter, which contains vital plant nutrients and, storing more carbon in soils would allow to recover the lost fertility. There is thus an urgent need to develop strategies to enhance crop WUE, mitigate human-induced greenhouse gas (GHGs) emissions and improve or sustain soil fertility for sustainable food systems and human wellbeing. Improved crop cultivars allow to produce more food with less water and sequester a larger amount of atmospheric CO_2. Breeding and deployment of water and carbon efficient crop cultivars is one of the most economical, effective and sustainable strategies to global food security and in minimizing human-induced GHGs.

Gaps of knowledge in crop selection

Despite numerous studies on WUE of staple cereal crops, there is yet little information on the extent of the variations in WUE or atmospheric C storage between the different cultivars and associated controlling mechanisms, which might allow the selection of drought-resilient varieties and to guide breeding programs. Yet, there is a need to decipher and identify the genetic variation for water use efficiency and carbon sequestration potential among genotypes of different cereal crops grown in multiple environments. This is crucial as it would allow direct selection and promotion amongst farmers of varieties with superior attributes for water use efficiency and carbon sequestration. Besides, the positive feedback of enhanced carbon storage in soils, such as increased water and nutrient retention for improved soil structure, reduced soil erosion and improved food production and water quality and availability in rivers and water tables, remains to be investigated.

PROJECT AIMS

In light of the above background, the specific objectives of the project were to:

- i validate data on water use efficiency and soil carbon sequestration potential of selected cultivars of wheat, maize and sorghum under several environments in SA.
- ii rank cultivars of each crop to advise farmers on which one to use for a given condition for sustained agricultural development.
- iii understand the link between WUE and soil carbon sequestration on one hand and plant traits and markers on the other hand to inform selection programs.
- iv build a capacity of post-graduate students and smallholder farming communities on water-use efficiency and soil carbon dynamics in the context of climate change.
- v quantify the contribution of indigenous and commercial crop varieties to water and global carbon credits.
- vi facilitate knowledge exchange for upcoming female and male scientists, members of staff and postgraduate students. Knowledge transfer activities will seek to enhance technology and knowledge sharing on the underlying plant-to-soil processes in plant-captured C translocation to soils, the associated plant genes for establishing crop breeding strategies and the best management packages for stabilizing soil C.
- vii initiate and strengthen partnerships between research-oriented institutions from Europe (France) and Africa (South Africa, Zimbabwe and Mozambique).

METHODS

Two main types of methodologies were used in the course of the project. The first one involves meta-analyses of previous studies in South Africa and worldwide. While several individual studies have been published on the water use efficiency of wheat, maize and sorghum, data have not, for the most part, been synthesized and validated, yet the global trends are still unknown. This project analysed results from multiple trials worldwide that quantified WUE of wheat, maize and sorghum cultivars and their variations. Studies investigating the C fluxes from the atmosphere to the soil during the growing cycle using C labelling for WUE estimation and the quantification of carbon inputs to soils were also assessed. Meta-studies inform on current trends and provide vital information on what hypotheses and results is to be expected from ongoing and new field trails. The present project also assessed the genetic diversity of a large set of genotypes of wheat, maize and sorghum, making available invaluable information that can assist to develop climate-smart and drought-adapted varieties. A higher number of germplasm collections were investigated for grain yield, biomass and carbon allocation from shoot to roots and drought tolerance based on complementary phenotypic and root attributes and high-density single nucleotide polymorphism (SNP) markers to select breeding parents. The genotypes were evaluated in field and greenhouse trials under drought-stressed and non-stressed conditions.

RESULTS

The main findings of the research project are outlined below:

Factors affecting crop WUE and carbon storage worldwide

The results showed that WUE decreased from a median of 1.48±0.07 kg m^{-3} for maize to 1.01±0.06 kg m^{-3} for wheat to 1.20±0.10 kg m^{-3} for sorghum (**Chapter 2**). The highest range in WUE between cultivars was found for maize with values between 0.3 kg m^{-3} for cultivars DK9089 and KCB to about 4 kg m^{-3} for SNK2147, which corresponded to a 13 times difference. There was a 4.7 times difference between the least (0.7 kg m^{-3} for Kaura) and most (3.3 kg m^{-3}; Sugargraze) efficient sorghum cultivars, and the difference increased to 25 times for wheat cultivars (0.2 for Karail in Australia to 5 for Pronta in South America). Moreover, WUE tended to positively correlate with grain yield (r=0.75 for maize; 0.65 for wheat) and phosphorus application rate (0.30; 0.72), but decreased with plant biomass (-0.55; -0.31). Surprisingly, the nitrogen application rate had an nonsignificant impact. These results important for making decisions on crop and crop cultivar selection in climate variability.

The review of meta-data on the impact of crop genotype on biomass allocation and carbon storage in cereals (**Chapter 3**) provided evidence of high intra-specific variation between maize and wheat biomass, carbon accumulation, and allocation to roots and shoots, demonstrating the importance of these genetic resources for the development of varieties with improved C sequestering potential. Overall, maize exhibited the highest plant biomass variability, followed by wheat and sorghum. The same trend was observed for root biomass, with maize ranking top, followed by wheat, and sorghum. The within-crop variability of all variables decreased with the increase in soil clay content, and tillage increased the variability in all cases except for shoot and plant biomass and C stocks. In our investigation, wheat presented the greatest potential for breeding to increase biomass production due to limited breeding targeted at carbon sequestration in the crop. Using wheat as a model crop for increasing carbon sequestration can go a long way in mitigating the effects of climate change. Maize and sorghum will also remain essential crops that can be used to support climate-smart agriculture. The present findings improve our understanding of how C is allocated within plant tissues and possibly to soils, and they may be used as selection criteria for breeding crop varieties with high C sequestration capacity.

Variability between cereal crop cultivars grown in South Africa

Agronomic traits

Chapter 4 highlighted significant differences in biomass production among sorghum genotypes ranging from 0.56 to 164.13 g plant^{-1}, grain yield (GY) ranging from 0.59 to 12.88 g plant^{-1}, and WUE ranging from 0.63 to 0.001 g plant^{-1} mm^{-1}. Genotype AS115 produced the highest GY (12.88 g plant^{-1}) compared to all other evaluated genotypes. Genotype SS27 had the highest shoot biomass (SB) (137.83 g plant^{-1}), root biomass (RB) (137.83 g plant^{-1}), plant biomass (PB) (164.13 g plant^{-1}), as well as the highest WUE. Grain yield exhibited positive significant correlation with harvest index (HI) and WUE GY ($p \leq 0.01$) for both wheat and sorghum. Overall, the sorghum genotypes that were identified to have high biomass production and WUE include AS115, AS134, AS251, AS132, and AS130, and these can be used as parental cultivars in breeding programmes, specifically targeting production for bioenergy and forage – since they produce very high biomass. With the new wave of renewable energy and bioenergy crops, substantial potential exists to scale up sustainable bioenergy production from the cultivation of some crops in southern Africa. A targeted breeding of sorghum for bioenergy production can feed into the drive of expanding biofuel production sustainably. Therefore, these genotypes can in fact, feed into bioenergy breeding programs. The top wheat families such as LM71 x BW152, LM75 x BW141 and LM70 x LM47, with the highest grain yield production, while using water efficiently, were identified and should be used to generate new breeding populations to develop more water-use efficient cultivars. This is in line with the market demand, and releasing these varieties may translate into good value for farmers. These will offer a dynamic increase in yield and will be regarded as the way forward and the first step in a new phase of cultivar development as far as the small grain cultivars in South Africa are concerned. So far, the new and early generation family we developed (F3 lines) showed an improved grain yield under drought stress by an average of 33% with a maximum of 58% obtainable for the family BW141 X LM71.

Carbon storage

Chapter 5 demonstrated that genotypes store more C in their shoots than their roots, and the selection of sorghum and maize genotypes based on biomass production and allocation will allow for a more effective selection of high-yielding and carbon sequestration potential. The genotypes that showed the highest potential for carbon sequestration for sorghum were SS27, AS138, AS134, AS203, and AS251; and for maize, were TZ-30, TZECOMP3DT/WHITEDTSTRSY-CZ, TZ-44, and TZE COMP5C7/TZE COMP39TCZ, while producing optimum grain yield and biomass. Several sorghum and maize genotypes offer higher soil C by increasing root biomass production under deep root systems. Based on the current findings, several sorghum and maize genotypes also increased C stock in shoots and roots. These findings support using sorghum and maize genotypes to improve soil carbon sequestration.

Candidate cultivars developed

Cultivars and new families with significant WUE, carbon sequestration and high biomass production potential were identified. Direct wheat crosses BW162 × LM75, BW152 × LM75, LM70 × LM75, LM71 × LM75 and LM26 × LM75 and reciprocal crosses LM48 × BW140, LM71 × LM26, LM70 × BW152, LM70 × BW141 and LM75 × LMBW152 are recommended for genetic advancement and cultivar development. The genotypes that showed the highest potential for carbon sequestration while producing optimum yield and biomass for sorghum were SS27, AS138, AS134, AS203, and AS251; and TZ-30, TZECOMP3DT/WHITEDTSTRSY-CZ, TZ-44, and TZE COMP5C7/TZE COMP39TCZ for maize. The high root biomass production of all the selected families and crop cultivars will contribute to carbon inputs through rhizodeposition in agricultural soils. It is recommended that the cultivars should be evaluated for net carbon contribution to the soil.

CONCLUSIONS

Innovation

In conclusion, the new candidate cultivars generated through the project, currently at F_3 generation, have shown enhance grain yield and water use efficiency under drought stress by an average of 33% with a maximum of 58% obtained for BW141×LM71 as compared to the best parent (LM48). The new breeds have the potential to enhance soil quality and carbon footprint and require further validation through dedicated multilocation field evaluations.

Insights on the mitigation of the human-induced GHGs in South Africa

The South African government has been proactive and devised policies to carbon stocks and associated GHG emissions in natural and semi-natural ecosystems. Agricultural land may be the place of shifts in management to sequester atmospheric C, and several strategies have been suggested over the last decades. However, strategies such as zero tillage have been shown less efficient, and cover crops do not seem to store as much C as previously thought. Here, we show a pragmatic and easy-to-access strategy to increase soil C in crop lands. The country has a land surface area of 1,220,000 km^2. Of this, around 11% or 12 million ha of the land is arable. Assuming all arable land in South Africa is cropped with cultivars with a 250% improved allocation to soils, as our project showed for the best wheat cultivar which we identified, the transfer of atmospheric CO_2 to soils of between 0,4 to 17 ton ha yr^{-1} for average cultivars would increase to 1 to 4,25 ton ha yr^{-1}, which would correspond to a net CO_2 offset for the whole country of 19,2 to 81,6 million tons, or **4,7 to 20,1% of the total South African 2022 CO_2 emissions of 405 million tons**. This will complement grassland rehabilitation in the country as documented in the project WRC2266, a much more difficult-to-implement strategy but with staggering benefits for soil C increase. Rangelands suffer from severe degradation with soil C stock losses of as much as 90% that can be replenished using improved grassland management involving short duration high-density grazing. Assuming up to 60% of South Africa's rangelands are degraded and losses of 30 to 50% in the top 0.3 m of the soil, the carbon sequestration potential could be 1.44 to 2.41 Gt. A sequestration rate of 3.5% (as reported in WRC2266) would correspond to 0.08 to 0.11 Gt C $year^{-1}$ or **53-72% of the total South African 2022 CO_2 emissions of 405 million tons. In sum, the cumulative offset by South African grasslands and croplands would be 58 to 92% of total C emissions.**

Future research

The present project pinpointed the importance of crop biomass production and unique genotypes with enhanced WUE and C storage into soils while maintaining high levels of grain yield. While cereal crops had previously been bred for high shoot yield and agronomic value, future research on cereals should focus on breeding strategies towards enhanced root biomass production. In order to develop the cultivars of the future with even higher WUE and C sequestration potential, high-precision root phenotyping and genotyping should be employed together with quantitative trait loci (QTL) analyses to ascertain the genetic determinants of root architecture and to direct the breeding. Such methods will be applied to the new cultivars we developed during the present project. The selected ideotypes should be tested in diverse field environments (multiple soil types and climates) to recommend superior high-performing and water and climate-smart crop cultivars to growers and the marketplace. The study is valuable in the face of increased CO_2 content in the atmosphere, which is expected to double in 2050 as forecasted in 1990.

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LIST OF ABBREVIATIONS

ACCI	African Centre for Crop Improvement
ANOVA	Analysis of variance
ARC/SA	Agricultural Research Council of South Africa
C	Carbon
^{13}C	Carbon 13 isotope
CO_2	Carbon dioxide
CT	Cultivation tillage
CV	Coefficient of variation
GY	Grain yield
KZN	KwaZulu-Natal
N	Nitrogen
$NH4_+$-N	Ammonium-nitrogen
NO3-N	Nitrate-nitrogen
NT	No tillage
P	Phosphorous
PB	Plant biomass
Pc	Plant carbon
Q1	25th Quartile
Q3	75th Quartile
r	Correlation coefficient
RB	Root biomass
Rc	Root carbon
Rcs	Root carbon stocks
SB	Shoot biomass
Sc	Shoot carbon
Scs	Shoot carbon stocks
SOC	Soil organic carbon
SSA	sub-Saharan Africa
ST	Subsoil tillage
UKZN	University of KwaZulu-Natal
WRC	Water Research Commission
WUE	Water use efficiency

LIST OF UNITS

Variable	Symbol	Unit
Grain yield	GY	g plant^{-1}
Harvest index	HI	%
Plant biomass	Pb	Mg/g ha^{-1}
Plant carbon content	Pcc	%
Plant carbon stock	Pcs	Mg/g C ha^{-1}
Root biomass	Sb	Mg/g ha^{-1}
Root carbon content	Rcc	%
Root carbon stock	Rcs	Mg/g C ha^{-1}
Root:shoot ratio of biomass	Rb/Sb	
Root:shoot ratio of carbon stock	Rcs/Scs	
Shoot biomass	Rb	Mg/
Shoot carbon content	Scc	%
Shoot carbon stock	Scs	Mg/g C ha^{-1}

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CHAPTER 1. INTRODUCTION

1.1 Background and motivation of the project

Agriculture is the economic backbone for the majority of countries in the sub-Saharan African (SSA) region (Diao *et al.*, 2010; Wang *et al.*, 2023). Improving agricultural productivity is important to ensure poverty reduction and food security in the region. However, agricultural productivity in SSA is challenged by climatic conditions, poor soils, pests and diseases (Tadesse *et al.*, 2019; Jayne and Sanchez, 2021). There is widespread water scarcity in Africa's arid and semi-arid regions, including South Africa, which has curtailed agriculture development. The average annual rainfall has decreased over time, and the distribution has become more erratic to support high-potential agriculture. The persistent drought and heat stresses in the region is associated with climate change (Fonta *et al.*, 2011; Jayne and Sanchez, 2021). Increasing agricultural production to support the food demand of the burgeoning population pressure in SSA will potentially exacerbate the already intense competition for water resources (Rosegrant *et al.*, 2009). Because of the higher frequency of extreme climatic events, the available freshwater resources are expected to experience intense siltation due to enhanced soil and stream bank erosion in river basins.

South Africa is one of water scarce countries in SSA. So far, the country has compensated for the shortages of water in some areas by increasing groundwater extraction, but this will only be temporary as this resource is finitely limited. There is a need to develop strategies for maximizing water productivity and improve crop production under harsh growing conditions. Selecting and developing water and carbon efficient crop cultivars is a strategy to support sustainable agriculture intensification to ensure food security (Raza *et al.*, 2012; Matthews *et al.*, 2013; Farooq *et al.*, 2019; Tian *et al.*, 2021). Primarily, this project seeks to identify genetic variation for water use efficiency and carbon sequestration potential among genotypes (varieties) of different cereal crops grown in multiple environments. This will facilitate selection of varieties with superior attributes for water use efficiency and carbon sequestration amid climate change and soil degradation challenges currently faced around the country. The project is premised on the interlink between water and carbon dynamics in the soil and the impact of carbon emission from croplands on atmospheric carbon concentration. Plants are the conduit between the atmosphere and the soil and play an irreplaceable role of transferring carbon to the soil. The positive impact of long-term storage of carbon in the soil include reduced atmospheric carbon concentration, increased water and moisture retention capacity of the soil and improved soil structure for nutrient and water recycling.

A previous WRC project (K5/2721; Water use efficiency and carbon sequestration potential of indigenous crops) that ended in 2020 in the KZN province showed that the relationship between plant, water use efficiency and soil C stocks is subject to complex interactions among soil, plant and climatic factors. The impact of environmental and soil conditions on these parameters are very important and this necessitates the need to conduct multi-location or multi-environmental trials to validate the environmental impact and also to enable the calculation of C and water use budgets at regional scale. This project seeks to investigate the water use efficiency and soil carbon sequestration capacity of maize, wheat and sorghum. These crops were selected based on their production and importance in the context of southern African agricultural systems. They occupy the largest area by annual crops and provide food to millions of people. In addition, being cereals of different types, they provide an overview and holistic approach to understanding water and carbon dynamics. Maize and sorghum are summer crops with a C4 photosynthetic pathway while wheat is a winter crop with a C3 photosynthesis. Wheat and maize have been reported to be highly sensitive to water shortage whereas sorghum is relatively tolerant to water and heat stress. The water use efficiency and carbon sequestration of these crops need to be assessed under different water availability scenarios in different environments to ascertain their potential and guide varietal selection. These crops have been in production for a long time and are adapted to the local conditions.

1.2 Project aims and objectives

The aim of this study was to evaluate water use efficiency and carbon sequestration potential of sorghum, maize and wheat in multi-environmental trials (Ukulinga research farm of KwaZulu-Natal in Pietermaritzburg, KwaZulu-Natal; Agricultural Research Council – Agricultural Engineering in Silverton, Gauteng; and Agricultural Research Council – Small Grain in Bethlehem, Free State (Figure 1.1). Simultaneous assessment of WUE, crop productivity and carbon sequestration for different cultivars of these three crops were carried out to fulfil these objectives. Specifically, the study evaluated biomass production, grain yield, C sequestration potential and water use efficiency of maize, sorghum and wheat varieties over a three-year period. The study sites selected for this research were guided by availability of ancillary infrastructure such as adequate security, access to roads and presence of weather stations. The specific objectives of the project were:

i to evaluate water use efficiency and soil C sequestration potential of sorghum varieties in comparison with maize and wheat varieties in multi-environmental trials.

ii to rank cultivars of each crop for advising farmers on which one to use for a given condition for sustained agricultural development.

iii to understand the link between WUE and soil carbon sequestration on one hand and plant traits and markers on the other hand to inform selection programs.

iv to build capacity of post-graduate students and smallholder farming communities on water-use efficiency and soil C dynamics in the context of climate change.

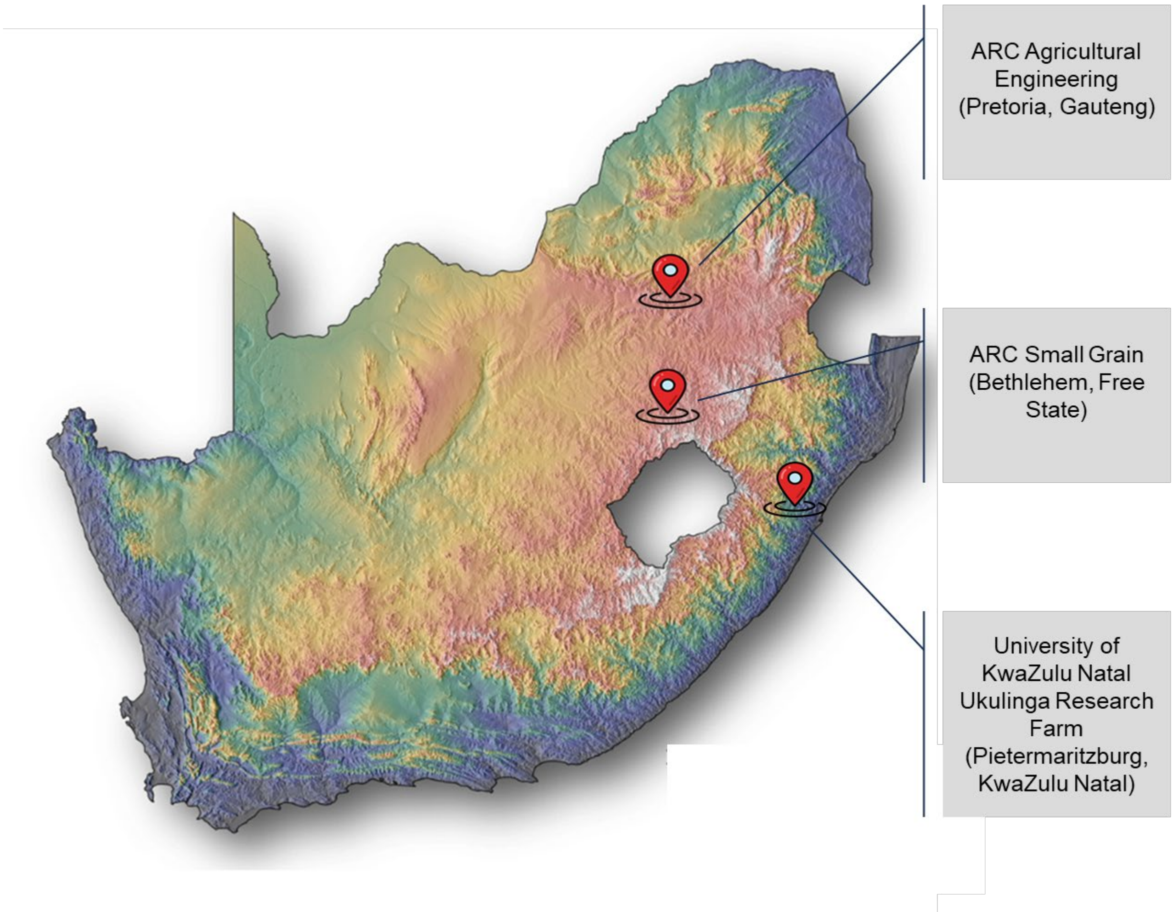

Figure 1.1 Field testing trial sites in Gauteng, Free State and KwaZulu-Natal provinces of South Africa.

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CHAPTER 2: A global perspective of factors affecting the water use efficiency of major cereals

Abstract

Cereals constitute the main source of energy for humans and water is a major limiting factor for grain yield. Despite numerous studies on water use efficiency (WUE) of main cereal crops, there is yet little information on the variations between the different cultivars and on main factors of control, which might allow selection of drought-efficient varieties and to better inform breeding programs. This study used data from 665 experiments around the world published in ISI journal papers to investigate the variations in WUE for grain yield between selected cultivars of maize, wheat and sorghum grown under different climatic and soil conditions. The results showed that WUE decreased from a median of 1.48±0.07 kg m^{-3} for maize to 1.01±0.06 kg m^{-3} for wheat through 1.20±0.10 kg m^{-3} for sorghum. The highest WUE range between cultivars was found for maize with values between 0.3 for DK9089 and KCB to about 4 for SNK2147, which corresponded to a 13 times difference. There was a 4.7 times difference between the least (0.7 for Kaura) and most (3.3: Sugargraze) efficient sorghum cultivars and the difference increased to 25 times for wheat cultivars (0.2 for Karail in Australia to 5 for Pronta in South America). Moreover, WUE tended to positively correlate with grain yield (r=0.75 for maize; 0.65 for wheat) and phosphorus application rate (0.30; 0.72) but decreased with plant biomass (-0.55; -0.31). Surprisingly nitrogen application rate had an insignificant impact. These results provide information that is important for making decisions on crop and crop cultivar selection in a context of climate variability. However, while there were limited information available on WUE for cultivars in conjunction with main controls, research studies are needed for improving the understanding of the mechanisms responsible for the observed high level of variability within cereal crops.

Keywords: climate variability, crop water use efficiency, crop management, photosynthetic prowess, soil water availability.

2.1 Introduction

Globally 80% of the agricultural land area is rainfed and droughts, i.e. periods of water scarcity or water absence, have long posed a major threat to food production (Beacham *et al.*, 2018; Zhang *et al.*, 2018). Because plants are immobile, they developed strategies to survive in harsh conditions of stresses (Yokota *et al.*, 2006). When the availability of water to plants is restricted, innumerable cellular processes are affected leading to reduced photosynthesis rate, decrease in stomatal conductance, transpiration rate and mesophyll conductance, plant above and below ground biomass thus leading to decreased grain yield (e.g. Allahverdiyev, 2016; Zargar *et al.*, 2017). For instance, plants exposed to water shortage reduce the net CO_2 uptake by leaves because of stomatal closure thus leading to a decrease in CO_2 concentration in the chloroplast. Hypothetically, irrigation could meet the gap between crops needs and what soil can provide to them as a result of rainfall and soil retention. This is what has been happening for decades in many arid and semi-arid areas where lack of soil water has been compensated by artificial supplementation of water pumped into rivers or water tables. However, the continuous depletion of these water bodies combined with escalating costs of setting and managing the pumping and distribution infrastructures hamper further expansion of irrigation in developing countries, and large historic subsidies to provide cheap energy to farmers in many countries are not sustainable. Furthermore, agriculture already accounts for 80-90% of total human freshwater consumption (Morison *et al.*, 2008), thus pointing to the need to find alternative solutions.

Selecting crops requiring less water to produce the same amount of biomass or food, is a credible option. Mbava *et al.* (2020) in the study of major world crops from 514 experiments indicated that the crop type has a significant effect on water use efficiency (WUE) for grain production, with cereals being the most water efficient as they produce on average 2.37 kg of dry grain per cubic meter (m^{-3}) of water. Cereals are followed by oilseeds (0.69 kg m^{-3}), fibre crops (0.45 kg m^{-3}) and legumes (0.42 kg m^{-3}). These authors also pointed out that amongst cereals, summer crops such as maize and sorghum are with 3.78 and 2.52 78 kg of dry grains per m^{-3} more water efficient than winter cereals such as wheat (1.02 kg m^{-3}), barley (1.21 kg m^{-3}) and millet (0.47 kg m^{-3}). The significant differences in WUE between maize and sorghum on one hand and wheat on the other hand is shown to originate from genetic differences affecting photosynthesis. Several authors such as Way *et al.* (2014) or Blankenagel *et al.* (2018)

have pointed out the increased CO_2 concentration in the cells of C4 crop types, which allow higher photosynthetic rates while reducing stomatal conductance.

Other authors such as Rampino *et al.* (2006) indicated the existence of within crops genetic differences leading to different response of cultivars to drought stress. For instance, White *et al.* (2015) and Kobata *et al.* (2018) indicates that modern wheat (*Triticum aestivum*) cultivars are highly susceptible to drought stress as compared to landraces because of compromised root systems that are less efficient in water acquisition. But yet little is known on the differences in WUE between cultivars of main crops. While breeding efforts have focused on improving yield potential, drought tolerance and WUE of crops for decades (e.g. Ruggiero *et al.*, 2017), the water scarcity issue has not been overcome. Identifying more WUE crop varieties might not only constitute a credible solution to adapt to water scarcity but also to inform on potential genetic gains. Indeed, while most of the yield related traits have reached their maximum genetic potential (Sadras & Lawson, 2011; Sanchez-Garcia, *et al.*, 2013) there is still potential for increased resistance to drought (Shamuyarira *et al.*, 2021).
Although several studies have reported on crop cultivars WUE, disparities between crop cultivars, soil type, climate, amount of water and nutrients applied during the growing season, make it difficult to compare WUE for grain yield. These numerous data provide however an opportunity for comprehensive analysis seeking to draw general understanding on crop cultivars WUE.

2.2 Methods and materials

2.2.1 Database preparation

Three electronic databases were used for literature search including Google Scholar, Scopus and Web of Science between September 2021 to November 2021. Key search terms for the literature search were “water use”, “WUE”, “water use efficiency”, “maize”, “sorghum” and “wheat”. The data collected was limited to only three cereal crops (maize, sorghum and wheat) while there was no delimitation on period of the studies. In order for studies to be included in the analysis, they had to report on WUE of crop cultivars. Where data for WUE was not available, WUE was collected based on water use and grain yield obtained by the cultivar. Names of authors, year of paper publication, country, region, crop name, tillage, water regime, nitrogen application and WUE were captured onto a database (Table 2.1). The final database consisted of 665 observations from 41 peer-reviewed ISI journal articles (Table 2.1).

Table 2.1: Summarised database compiled using data collected from ISI journal papers showing references (authors and years) and averages of water use efficiency (WUE) and different treatments applied during the experiments

Authors	**Country**	**Region**	**Crop Name**	**Tillage**	**Water regime**	**N application**	**Mean WUE**
Abbate *et al.* (2004)	Argentina	South America	Wheat	CT	Non-stress	High	4.67
Abuarab *et al.* 2013	Egypt	Africa	Maize	CT	Non-stress	High	5.08
Ajeigbe *et al.* (2018)	Nigeria	Africa	Sorghum	CT	Non-stress	Medium Low High	1.11
Barbieri *et al.* (2012)	Argentina	South America	Maize	NT	Drought	Low	1.50
Barraclough *et al.* (1989)	United Kingdom	Europe	Wheat		Drought	Low	1.05
Chennafi *et al.* (2006)	Algeria	Africa	Wheat	CT	Drought	Low	0.94
Chimonyo *et al.* (2015)	South Africa	South Africa	Sorghum	CT	Drought	Medium	0.39
Conley *et al.* (2001)	USA	North America	Sorghum	CT	Non-stress	Medium	2.82
Dağdelen *et al.* (2005)	Turkey	Asia	Maize	NT	Non-stress	High	2.09
Entz and Fowler (1989)	Canada	North America	Wheat	NT	Non-stress	Low	0.88
Fardad and Pessarakli (1995)	Iran	Asia	Wheat		Drought	Low	0.34
Fischer (1980)	Australia	Australia	Wheat		Drought	Low	0.40
Gao *et al.* (2008)	China	Asia	Maize	NT	Non-stress	Low	2.95
Hadebe *et al.* (2017)	South Africa	South Africa	Sorghum	CT	Drought	High	0.87
Hernández *et al.* (2015)	Argentina	South America	Maize	CT	Drought	High Low High	2.02
Howell *et al.* (2014)	USA	North America	Maize	CT	Drought	Medium	1.92
Igbadun *et al.* (2008)	Tanzania	Africa	Maize	CT	Drought	High	0.61
Kanani *et al.* (2016)	Iran	Asia	Maize	CT	Non-stress	High	2.84
Kang *et al.* (2001)	China	Asia	Wheat	CT	Non-stress	High	1.10
Kuscu and Demir (2013)	Turkey	Asia	Maize	CT	Drought	Medium	1.34
KUSCU *et al.* (2012)	Turkey	Asia	Maize		Non-stress	High	1.70
Luo *et al.* (2020)	Kenya	Africa	Wheat	CT	Drought	Low	1.18
Mbanyele *et al.* (2021)	Zimbabwe	Africa	Maize	CT RT	Drought	Medium Low	2.13
Mengistu *et al.* (2015)	South Africa	South Africa	Sorghum	CT	Non-stress	High	3.90
Meskelu *et al.* (2014)	Ethiopia	Africa	Maize	CT	Drought	Low	1.88
Miriti *et al.* (2012)	Kenya	Africa	Maize	CT RT	Drought	Low	0.45
Mohamed and Monem (1994)	Austria	Europe	Wheat		Drought	Low	0.67
Musokwa *et al.* (2020)	South Africa	South Africa	Maize	CT	Drought	Low	1.64

Siddique *et al.* (1990)	Australia	Australia	Wheat	CT	Non-stress	Medium	0.88
						High	
						Medium	
Srivastava *et al.* (2019)	Ethiopia	Africa	Maize		Drought	Low	0.75
				CT			
				NT			
				RT			
Su *et al.* (2006)	China	Asia	Wheat	ST	Drought	High	1.16
Tari (2016)	Turkey	Asia	Wheat	CT	Non-stress	High	1.68
				CT			
				NT			
				RT			
TerAvest *et al.* (2015)	Malawi	Africa	Maize	ST	Non-stress	High	0.48
Tolk and Howell (2003)	USA	North America	Sorghum	CT	Drought	Low	1.67
Tsubo *et al.* (2003)	South Africa	South Africa	Maize	CT	Non-stress	High	3.78
						Medium	
Zhang *et al.* (1998)	Syria	Asia	Wheat	NT	Drought	Low	1.05
						High	
						Medium	
Oweis *et al.* (2000)	Syria	Asia	Wheat	CT	Non-stress	Low	0.76
						High	
Paolo *et al.*(2007)	Italy	Europe	Maize	NT		Low	1.86
Payero *et al.* (2008)	USA	North America	Maize	NT	Non-stress	High	1.74
Payero *et al.* (2009)	USA	North America	Maize		Drought	High	1.50
Rusere *et al.* (2012)	Zimbabwe	Africa	Maize	NT	Drought	Low	1.69

2.2.2 Definitions of WUE and study variables

Table 2.2 provides definitions of variables that were used in this study. In the current study, WUE is defined as the amount of grain yield produced per unit volume of water used (kg m^{-3}) during the growing seasons for the crops. Grain yield is the amount of grain produced per unit area by the crops (kg ha^{-1}). The country is the geographical area in which the experiments in the study were conducted. Continents in which the experiments were carried out were referred to as region. Tillage is the method of land preparation used for growing the different crops. No till (NT) systems is where crops are planted without any soil disturbance compared to conventional tillage where deep ploughing and overturning of the soil, and removal of all crop residues from the seedbed are carried out. The water regime refers to the level of water applied to crops. Two water regimes, drought stressed and non-stressed, were considered for this study. Non-stressed treatments are those where adequate moisture was supplied for plant growth. Drought stress treatments involved supply of water in insufficient amounts to support optimum growth. Nitrogen (N) application is the level of added nitrogen applied to the soil in the growing season of the crop. Low N application rates were below 50 kg ha^{-1} N, medium rates were between 50 and 100 kg ha^{-1} N and high N application rates were above 100 kg N ha^{-1}.

Table 2.2: Definitions of the environmental factors, water use efficiency, grain yield and water use efficiency as used in the analysis

Environmental factors	Symbols	Units	Definitions
Water use efficiency	WUE	kg m^{-3}	Amount of yield per unit volume of the amount of water received in the plot
Grain yield	GY	kg ha^{-1}	Grain yield yielded when the crop had matured
Region			Continents in which the experiments were carried out
Water regime			Water levels received by a crop
Drought-stress			Insufficient water to promote optimum growth of the crop
Non-stress			Adequate moisture without any significant moisture stress to the crop
Nitrogen (N) fertilizer			Added nitrogen applied to the soil in the growing season of the crop
Tillage			Method of land preparation used for growing the different crops
No till (NT)			Land were a crop was planted without any soil disturbance
Reduced tillage (RT)			Minimum tillage without turning over the soil
Subsoil tillage (ST)			Minimum tillage to break the hardpan without turning over the soil

Environmental factors	Symbols	Units	Definitions
Conventional tillage (CT)			Deep ploughing or harrowing of the soil involving overturning the soil and removal of all plant residues from the seedbed
Mean annual precipitation	MAP	mm $year^{-1}$	Long-term (at least 30 year) mean precipitation per year for the study location from the papers
Mean annual air temperature	MAT	°C $year^{-1}$	Long-term (at least 30 year) mean temperature per year for the study location from the papers
Longitude	LONG	°	Longitude of the midpoint of study site as given in papers
Latitude	LAT	°	Latitude of the midpoint of study site as given in papers
Altitude	Z	m.a.s.l	Average elevation above sea level of the study site as given in the papers
Soil bulk density	BD	g cm^{-3}	Bulk density of the top soil layer as given in papers
Total Water	TW	mm	Total amount of water received by the crop during the full crop cycle (i.e. precipitation + irrigation)
Clay content	Clay	%	Average clay content (or fine textured soil particles) of the top soils in the plot
Silt content	Silt	%	Average silt content (or medium textured soil particles) of the top soils in the plot
Sand content	Sand	%	Average sand content (or coarse textured soil particles) of the top soils in the plot

Kg = kilogram, m.a.s.l = metre above sea level, ha = hectare

2.2.3 Data analyses

Descriptive statistics (minimum, maximum, median, mean, SEM: standard error of mean, quartile 1 and quartile 3 representing 25th and 75th percentiles, respectively, skewness (Skew), kurtosis (Kurt) and coefficient of variation (CV%) were calculated for all study variables. Mean WUE values were computed for the different crops and environmental factor classes. In addition, bivariate correlations based on Pearson correlation coefficients and multivariate associations based on principal component analysis (PCA) were computed using R software. PCAs convert non-linear factors and variables into linear combinations called principal components (Jambu, 19981).

2.3 Results

2.3.1 General statistics of environmental variables and WUE

In total, 665 observations on WUE were collected in the database (Table 2.3). The overall mean WUE was 1.46 kg m^{-3} and exhibited variation across the different treatments. The highest mean WUE (1.69 kg m^{-3}) was computed for the medium nitrogen fertiliser treatment followed by high nitrogen fertiliser treatment (1.58 kg m^{-3}). The no-tillage system exhibited higher WUE (1.54 kg m^{-3}) than conventional tillage (1.27 kg m^{-3}) while the drought stressed water regime had higher WUE (1.49 kg m^{-3}) than non-stress conditions (1.43 kg m^{-3}). Maize had the largest sample size with 315 observations followed by wheat with 260 observations (Table 2.4). The mean WUE was highest for wheat at 1.17 kg m^{-3} compared to 1.70 kg m^{-3} for maize and 1.40 kg m^{-3} for sorghum (Table 2.4). WUE ranged between 0.18 kg m^{-3} recorded for maize and sorghum to 8.7 kg m^{-3}.

Table 2.3: Summary statistics of water use efficiency (WUE) of all crops under different tillage and N fertiliser application treatments

Statistics	Overall	DS	NS	CT	NT	High N	Medium N	Low N
Observations	665	390	272	428	98	269	141	210
Mean	1.46	1.49	1.43	1.27	1.54	1.58	1.69	1.17
Median	1.16	1.18	1.09	1.14	1.25	1.20	1.40	0.92
Minimum	0.18	0.18	0.18	0.18	0.18	0.21	0.21	0.18
Maximum	8.70	8.70	7.89	8.70	2.95	8.70	7.40	7.40
Quartile 1	0.81	0.89	0.72	0.84	0.81	0.98	0.88	0.64
Quartile 3	1.69	1.69	1.67	1.65	1.69	1.54	2.03	1.45
Standard deviation	1.16	0.99	1.36	1.32	0.60	1.35	1.18	0.87
Standard error of mean	0.04	0.05	0.08	0.06	0.06	0.08	0.10	0.06
Coefficient of variation	79.16	69.38	91.03	85.63	46.98	85.14	69.73	73.75

DS=drought stressed, NS=non-stressed, CT=conventional tillage, NT=no=till, N=nitrogen

Table 2.4 Summary statistics of water use efficiency (WUE) of maize, sorghum and wheat

Statistic	Overall	Maize	Sorghum	Wheat
Observations	665	315	90	260
Mean	1.46	1.70	1.40	1.17
Minimum	0.18	0.18	0.21	0.18
Quartile 1	0.81	0.93	0.71	0.80
Median	1.16	1.48	1.20	1.01
Quartile 3	1.69	1.94	1.66	1.20
Maximum	8.70	7.89	4.64	8.70
Standard deviation	1.15	1.25	0.95	1.03
Standard error of mean	0.04	0.07	0.10	0.06

2.3.2 Variation in WUE across the world and different soil textures

Water use efficiency varied across different growing regions of the world (Figure 2.1A). South America had the highest mean WUE of about 3 kg m^{-3} followed by South Africa and Europe with nearly 2 kg m^{-3}. Africa and North America had comparable WUE while Australia had the least. Among the crops, maize grown in South Africa and Asia had higher WUE compared to maize in the other regions. Similarly, sorghum grown in South Africa was comparably more efficient at water use compared to the other regions. The WUE of wheat was highest in South America and Australia.

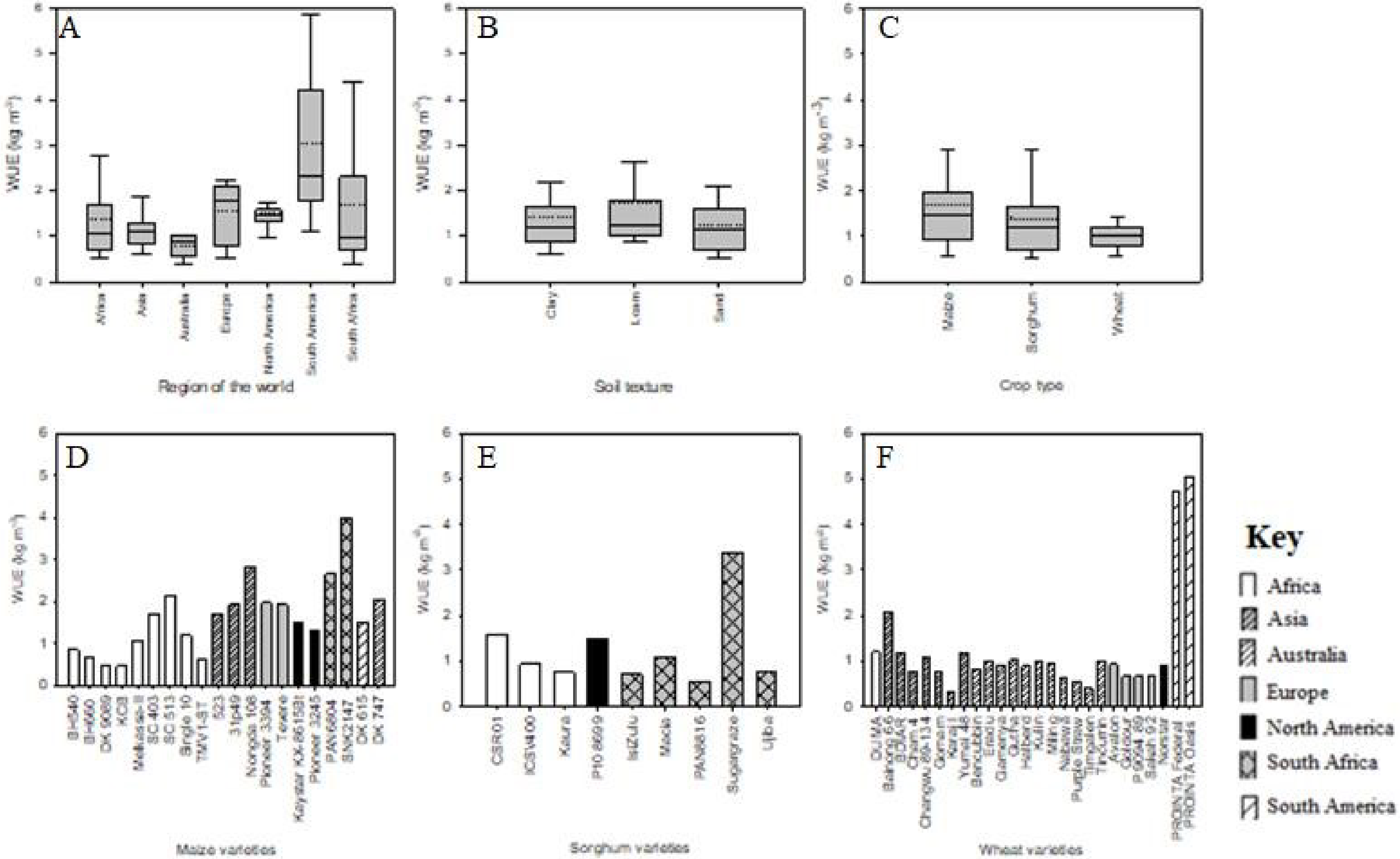

Figure 2.1 :Water use efficiency (WUE) of different crops measured across different parts of the world under diverse treatments

Water use efficiency also responded to differences in soil texture (Figure 2.1B). Boxplots showed that WUE was highest in loam soil followed by clay soils. On average, WUE in loam soil was about 2.1 kg m^{-3}, which was significantly higher than 1.6 and 1.32 kg m^{-3} recorded in clay and sandy soils, respectively.

2.3.3 *Impact of crop type on WUE*

The boxplot display showed that maize had the highest WUE of 1.70 kg m^{-3} (Figure 2.1C). Sorghum had the next highest WUE of 1.50 kg m^{-3} and wheat had the least WUE at 1.2 kg m^{3}. The WUE showed significant variation among different varieties of the same crop. For maize, varieties SNK2147 and PAN6804 cultivated in South Africa and varieties Nongda 108 cultivated in Asia were the most efficient at using water with WUE above 2.5 kg m^{-3} (Figure 2.1D). Other maize varieties such as SC 513 grown in Zimbabwe and the DK 747 cultivated in South America had favourable WUE of around 2 kg m^{-3}. Most of the maize varieties with the lowest WUE were grown in Africa. The highest WUE among sorghum varieties was 3.5 kg m^{3}, which was recorded for Sugargraze, variety grown in South Africa (Figure 2.1E). Varieties CSR01 and P10 8699 were the next best sorghum varieties with WUE around 1.5 kg m^{-3}. Among wheat varieties, Prointa Oasis and Prointa Federal had the highest WUE of 5.2 and 4.8 kg m^{-3}, respectively (Figure 2.1F). The next highest WUE of about 2.2 kg m^{-3} was found in a wheat variety Bainong 66 grown in Asia while the rest of the varieties had similar WUE of about 1.0 kg m^{-3} despite their production region.

2.3.4 *The impact of tillage, fertiliser and water treatments on WUE*

Different agronomic practices had influence on WUE as depicted in Figure 2.2. No-tillage system had higher WUE than the conventional tillage system (Figure 2.2A). The highest WUE was obtained where intermediate nitrogen application rates were used followed by high nitrogen application (Figure 2.2B). The drought stressed treatments induced higher WUE compared to non-stressed treatments (Figure 2.2C). The multivariate analysis showed that maize had higher GYD in conventional tillage while sorghum and wheat tended to have higher WUE values (Figure 2.3). In no-tillage systems, maize exhibited both high WUE and GYD compared to sorghum and wheat. Maize also exhibited the highest WUE and GYD with high N fertiliser application (Figure 2.4). When N fertiliser is applied mildly, WUE and GYD were found to be higher in sorghum and wheat, respectively, compared to maize. Under low N availability, GYD was highest in sorghum while WUE was higher in wheat. Sorghum tended to have higher WUE and GYD under drought stress conditions compared to maize or wheat (Figure 2.5). The GYD was highest in maize under non-stress conditions while wheat was inferior to both crops under all the water availability scenarios.

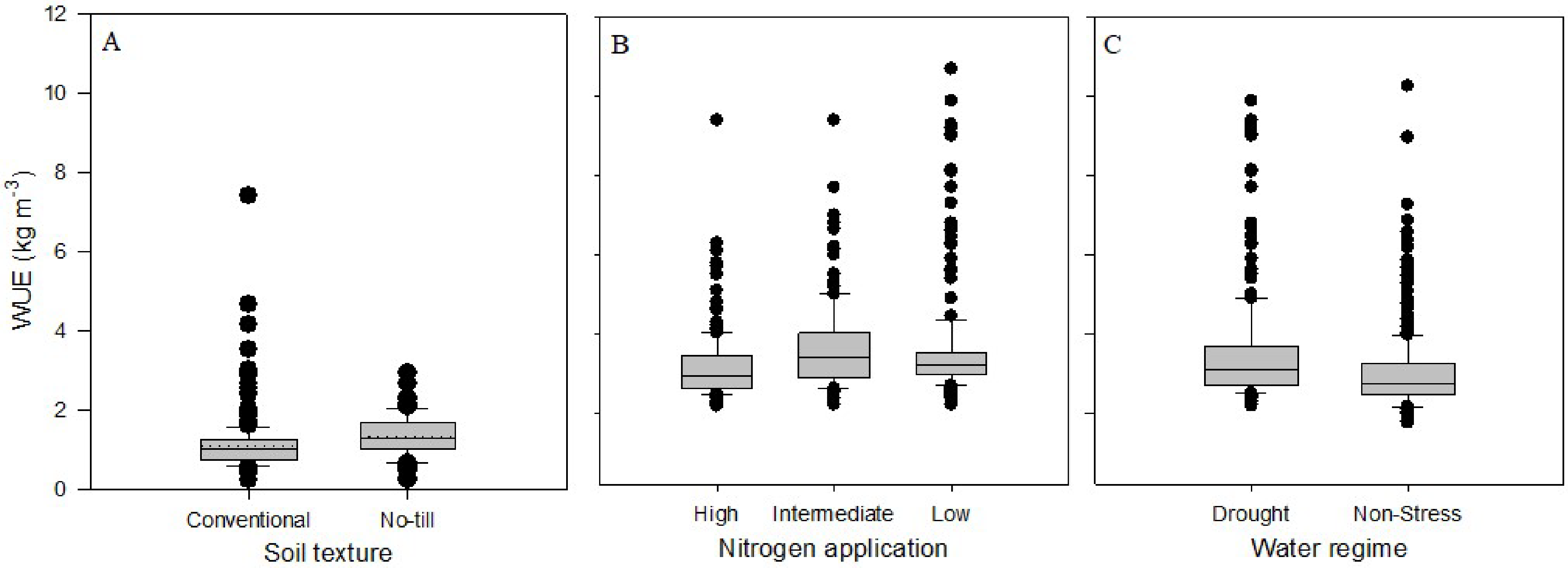

Figure 2.2:Water use efficiency of different crops measured under contrasting tillage, nitrogen application rates and water availability

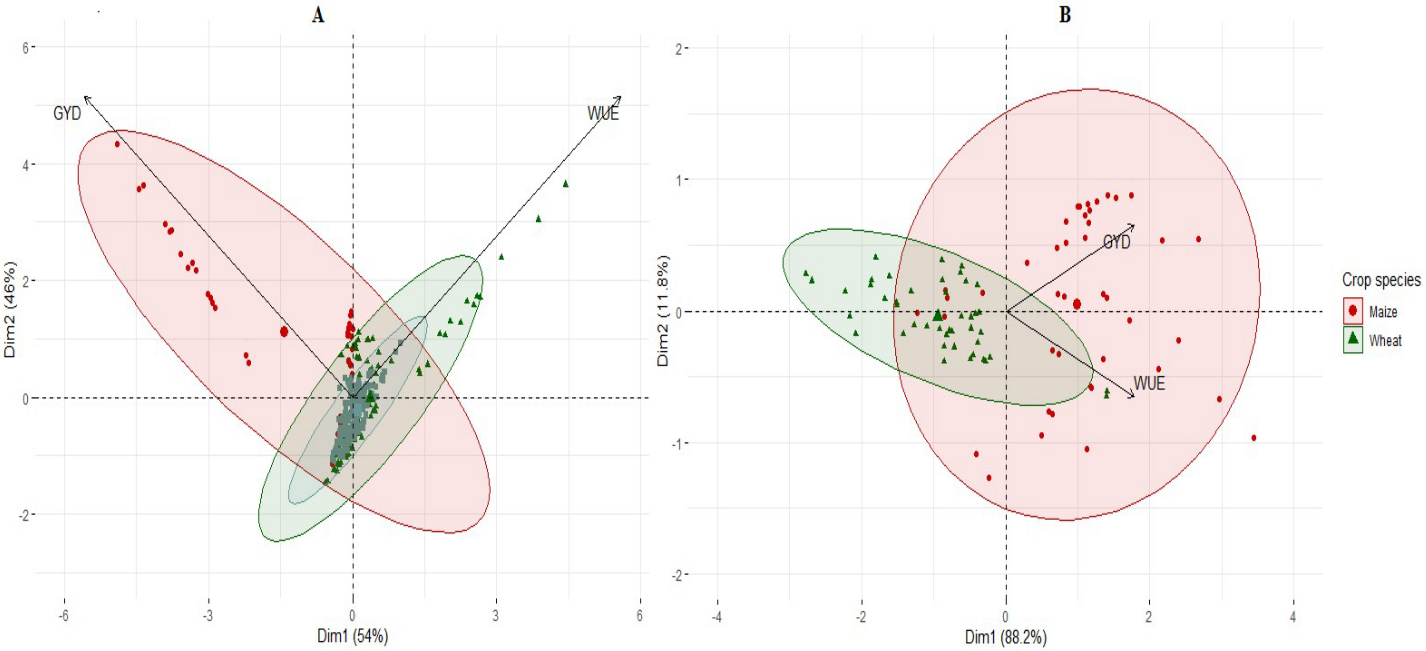

Figure 2.3**:** Comparison of water use efficiency (WUE) and grain yield (GYD) of crops under A) conventional and B) no-tillage

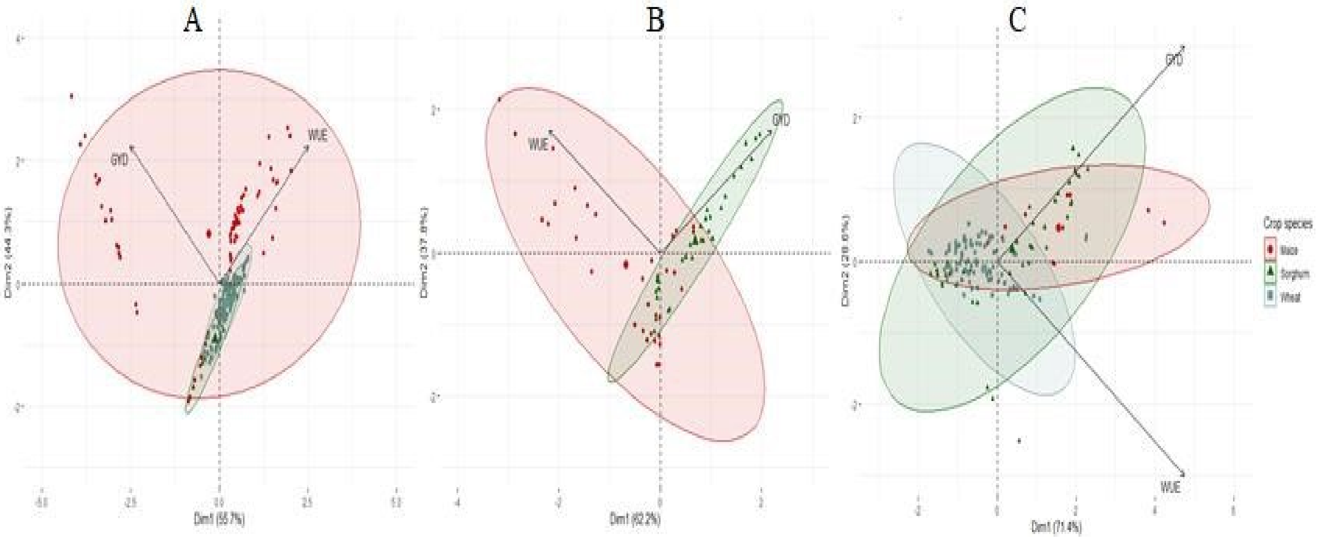

Figure 2.4: Comparison of water use efficiency (WUE) and grain yield (GYD) of crops under A) high B) medium and C) low N fertiliser application.

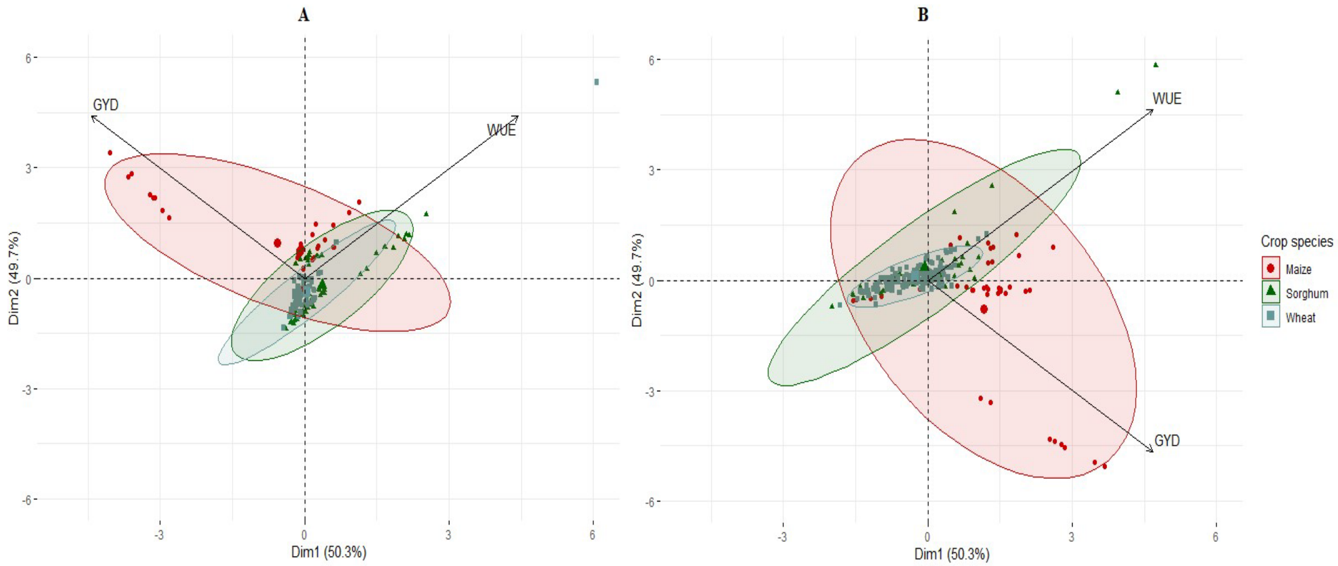

Figure 2.5: Comparison of water use efficiency (WUE) and grain yield (GYD) of crops under A) non-stress and B) drought stressed conditions.

2.3.5 *Correlations between environmental factors and WUE*

The correlations between WUE and other variables was assessed per crop (Table 2.5). Nitrogen availability exhibited positive correlations with WUE. Overall, the association between WUE and N was 0.21 ($p<0.001$) while it was 0.24 ($p<0.05$) for sorghum and 0.46 ($p<0.01$) for wheat. Water used was negatively associated with MAP for maize ($r=-0.18$, $p<0.05$) and sorghum ($r=0.49$; $p<0.001$). Overall, MAT was positively associated with ($r=0.20$; $p<0.001$) and sorghum ($r=0.49$; $p<0.001$). For maize, WUE was negatively associated with MAT ($r=-0.29$; $p<0.001$). Overall, GYD and WUE were positively correlated ($r=0.41$, $p<0.001$). WUE and GYD were positively correlated in sorghum ($r=0.31$; $p<0.001$) and wheat ($r=0.53$; $p<0.05$) (Table 2.5). Principal components accounted for49.1% of the total variation. The first two principal components with PC1 and PC2 accounting for 32.4 and 16.7%, respectively (Figure 2.6). PC1 was positively associated with amount of water used, and soil P and K contents and while soil organic nitrogen was negative associated with PC1. Grain yield and WUE were positively correlated with PC2 whereas SOC was negative associated with PC2.Maize exhibited wider dispersion along the PC1while sorghum was more correlated to PC2. Wheat was distributed even along both PC1 and 2. Higher amounts of water were applied to maize, which exhibited high GYD and WUE. Therefore, the results of this PC analysis implied that GYD and WUE were high in maize and increased with high organic matter content. These associations are in general agreement with the Pearson correlation coefficients presented in Table 2.5.

Table 2.5: Correlations between WUE and other variables for maize, sorghum and wheat across the world

Variable Nitrogen	Overall 0.29***	Maize 0.12*	Sorghum 0.31*	Wheat 0.56***
Latitude	0.02	0.34***	-0.81***	-0.09
Longitude	-0.54***	-0.15	-0.06	-0.06
Altitude	-0.13*	-0.23*	-0.48**	0.01
MAP	0.02	-0.18*	-0.48**	0.43***
MAT	0.20***	-0.29***	-0.48**	0.02
Sand	-0.21*	-0.57***	-	-0.27
Silt	-0.20	0.59***	-	0.27
Clay	0.27**	0.15*	-	0.27*
BD	0.45***	0.69***	-	0.32**
pH	0.87***	0.88***	-	-
OM	0.54***	0.44*	-	0.24*
SOC	0.41	0.50	-	-
SON	0.22	0.44*	-	0.39**
SP	0.71***	-0.44*	-	0.37***
SK	0.16	-0.44*	-	-0.48*
Water used	0.16**	0.31***	0.57***	0.19*
GYD	0.59***	0.64***	0.13	0.65***

MAP=mean annual precipitation; MAT=mean annual temperature; sand; silt and clay content=determinants of soil texture; BD=bulk density; pH=soil acidity or alkalinity; OM=organic matter content; SOC=soil organic carbon; SON=soil organic nitrogen; SP=soil phosphorous; SK=soil potassium; water used=amount of water applied per treatment

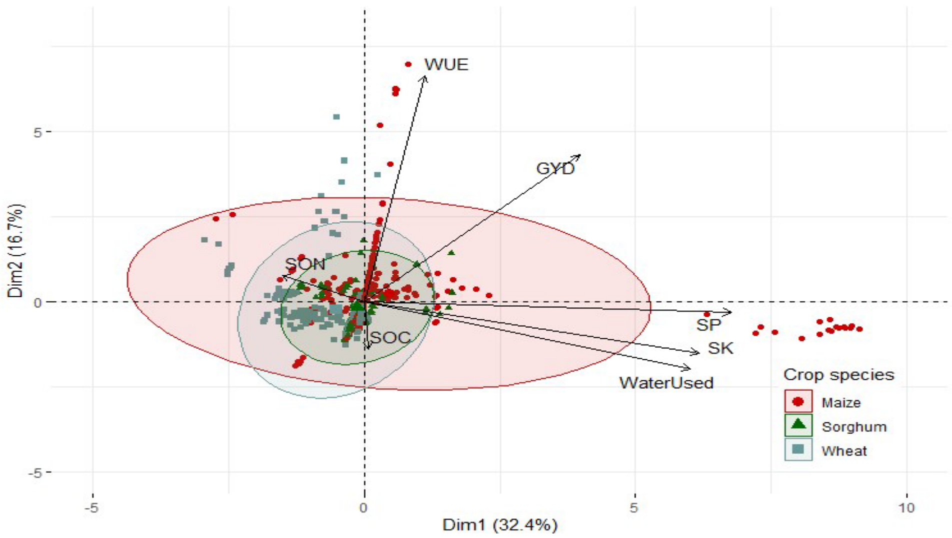

Figure 2.6: Multivariate relationships among different variables for maize, sorghum and wheat across different agronomic practices.

2.4 Discussion

2.4.1 *Crop and varietal differences in WUE*

The variation in WUE exhibited by the different crops shows that WUE is genetically controlled. Maize has been reported to be highly efficient at capturing solar radiation and utilisation of resources such as water and nutrients (Amanullah and Stewart, 2013). The high efficiency in resource utilisation is rendered by wide leaf area and ability to accumulate biomass compared to other cereals such as sorghum and wheat. Maize and sorghum have highly efficient C4 photosynthetic system compared to wheat. Studies have generally shown that C4 plants tend to be more water use efficient than C3 species under both natural and managed ecosystems (Blenkenagel *et al.*, 2018; Way *et al.*, 2014; Zwart and Bastiaanssen, 2004). The lower WUE exhibited by wheat compared to maize and sorghum could be linked to grain quality. Generally, crops that have higher protein and oil content require more water and energy during grain, which reduces their WUE in comparison to crops with high carbohydrate content (Munier Jolain and Salon, 2005). Wheat was found to have higher protein content (12.2%) compared to sorghum (9.1%) and maize (7.4%) (Robet *et al.*, 2020), which could have led to more water usage per unit grain produced by wheat. However, WUE was also affected by varietal differences. In South Africa, the production of maize varieties such as SNK2147 and PAN6804 with high WUE is important due to water shortage that are frequently experienced in the country. South Africa is categorised among countries with serious was shortages due to declining rainfall and poor soils. Likewise, maize variety SC 513 grown in Zimbabwe is adapted to low rainfall in the southern Africa region while the DK 747 maize variety cultivated in Argentina (South America) would probably be suited to acidic soils. The high WUE exhibited by Sugargraze, a sorghum variety grown in South Africa and CSR01 and P10 8699 varieties of sorghum grown in other parts of the world also exhibit varietal differences in variation and differences in adaptation. These varieties were developed for their specific environments, which enables them to maximize water usage. The Prointa Oasis and Prointa Federal wheat varieties interestingly have high WUE because they are grown in high input and intensive management systems in South America. In other regions such as Europe, the WUE of wheat is reduced by extremely cold temperature that significantly slow down biological processes of grain filling. Usually, winter wheat is grown over a longer period in Europe compared to the spring wheat varieties that dominate warmer regions such as sub-Sahara Africa and South America.

2.4.2 *Variation in WUE across the regions of the world*

However, WUE was also influenced by the region in which the crops were grown. Generally, WUE increases from high rainfall areas with low temperature to low rainfall areas with high temperature. The high water use efficiency recorded in South America and South Africa could be attributed to arid conditions compared to Europe. The studies from Argentina were from the Cordoba Province, which falls within the sub-tropical Chaco and semi-dry Pampas provinces (Seiler *et al.*, 2007). In South Africa, the studies were carried out around Pietermaritzburg, Bloemfontein and Pretoria. Pietermaritzburg is characterised by high summer temperatures while Bloemfontein and Pretoria are generally dry regions. Previously, WUE was found to be higher in drier conditions because C4 species such as maize and sorghum are the dominant species cultivated in these regions (Sage and Sage, 2013). For instance, the eastern seaboard of South Africa is dominated by C4 species that account for 74% of the flora supported by summer rainfall unlike the south-western tip around Cape Town that has a Mediterranean climate with winter rainfall where C4 account for less than 10% of the flora (Sage and Sage, 2013). Similarly, high WUE was recorded for crops grown in Australia including C3 species such as wheat because Australia experiences high temperatures and low rainfall conditions.

Specifically, WUE exhibited positive association with MAT and negative correlation with MAP, confirming that WUE tends to be higher in drier and hotter areas. Hot temperatures induce a serious of responses such as leaf rolling, waxy cuticle covering and use of the C4 photosynthetic pathway. The WUE is achieved by stomatal closure to reduce water loss but maintaining high concentration of CO_2 for photosynthesis (Killi *et al.*, 2017; Riboldi *et al.*, 2016). The bundle sheath in C4 plants is specially designed for maintaining high photosynthetic activity under high temperature and low moisture availability, which partially explains why sorghum and maize have higher WUE than wheat in more arid and hotter climates. Basically, under harsher conditions plants invoke drought and heat stress coping mechanism such as drought escape, avoidance and tolerance. These mechanisms enable plants to achieve higher WUE despite a reduction in absolute biomass production. However, the level at which these mechanisms are invoked vary from across species and genotypes. Sorghum is relatively more drought and heat tolerant compared to wheat and maize (Bhattaraj *et al.*, 2019).

2.4.3 The *effects of tillage, fertiliser and water treatments on WUE*

In conventional tillage, the higher grain yield production by maize compared to sorghum and wheat exhibited the genetic superiority of maize on biomass production. However, the grain yield production by maize is achieved at higher water costs as shown by its tendency to have lower WUE than sorghum and wheat. Maize is known to have high input requirements than sorghum (Jankowski *et al.*, 2020), which probably increased the water usage by maize under conventional tillage. Water conservation is low under conventional tillage, which contribute to low WUE especially by crops such as maize and wheat that have inherently high affinity for water resources. In no-tillage system, maize exhibited a tendency to have the highest values for both grain yield production and WUE partly due to its superiority and soil conservation. As already alluded, in general, maize has high biomass production potential compared to sorghum and wheat. Its superiority is further boosted by the water conservation capacity in no-tillage system. Compared to conventional tillage, no-tillage stores and retains soil moisture for longer due to non-disturbance of the soil (TerAvest *et al.*, 2015). It also provides soil cover to reduce direct loss of soil moisture by evaporation. Combined, these processes ensure that more water is available for plant growth and development. So, crops are likely to attain their genetic potential for grain yield production using less water resources in no-tillage systems. When high amounts of nitrogenous fertiliser are applied, maize becomes effective at grain production and water usage resulting in both high grain yield and WUE observed. Maize has superior resource conversion rates under optimal conditions compared to sorghum and wheat. Amanullah and Stewart (2013) also found that maize was more superior at grain production under optimal conditions compared to other cereals such as sorghum and legumes such as soybean. Under mild or low N application rates, maize had the lowest GYD and WUE compared to wheat and sorghum because maize is more sensitive to resource deficit. Maize is adapted to high input systems and suffers significant yield loss when resources are limited (Jankowski *et al.*, 2020). However, wheat is also known to be sensitive to nitrogen and water stresses. The impact of N would be expected to be higher on grain quality in wheat because it is required for protein synthesis. Under conditions of low water availability, the superiority of sorghum is exhibited by its high grain yield production and WUE compared to the maize and wheat. Sorghum possesses a dense root system capable of exploring the soil volume for moisture and have drought tolerance mechanisms, which combine to achieve high grain production and WUE. Expectedly, maize excelled in grain yield production and WUE in optimal water availability conditions while wheat was mostly the last compared to the other two crops showing its lower genetic potential. Amouzou *et al.* (2019) reported that simulation models predicted that WUE in maize would decrease by, on average, 18% while nitrogen mobilisation would decrease by 14% under combined water and nitrogen deficiencies. In comparison, sorghum was projected to incur on average 13% decrease in WUE and between 17% loss in nitrogen mobilisation.

2.4.4 ***Effects of soil physical and chemical properties on WUE***

Water use efficiency also responded to differences in soil texture. The positive association between WUE and clay content is attributable to improved water holding capacity of clays soils. Unlike sandy soils that suffers from high percolation or evaporation rates, clayey soils have enhanced capacity for moisture retention, which provides crops with moisture for extended periods to produce high grain yield (Tahir and Marschner, 2017). However, clayey soils are prone to crusting and cracking when exposed to alternate wetting and drying events. The crusting or susceptibility to water logging in clayey soils have adverse impact on crop growth and productivity. High clay content in soils can lead to waterlogging and suppression of root metabolic processes (Greenway *et al.*, 2006; Morales-Olmedo *et al.*, 2015) while crusting hinders root development. Resultantly, crops perform better in loam soils that have a balance between aeration and moisture availability. Loam soils have a balance of fine and coarse soil particles that provide water retention and air movement and do not hinder root growth for plant productivity (Tahir and Marschner, 2017). Sandy soils are too coarse and porous to maintain plant available water causing impeded plant growth and low WUE. The high WUE achieved by plants grown in loam soils is concomitant with the favourable soilwater dynamics likely to exist in loam soils. High WUE for other crops including cereals and legumes were found in loam soils (Katerji *et al.*, 2009).

There was a trend showing that WUE increased with soil pH. In general, soil acidity is more detrimental to plant growth compared to alkalinity. As a result, plant growth and grain production would improve with rising alkalinity from acidic soils and therefore improve WUE. In most cases, agricultural soils suffer from acidity due to the exorbitant application of inorganic fertilisers. Liming, which is the application of dolomitic or calcium-based sulphates, is carried out to increase soil pH in agricultural soils. Improved crop growth and grain production are realised following liming depending on other attendant factors such as water availability and crop species (Holland *et al.*, 2018). Similarly, WUE was positively associated with soil organic matter content (SOM), which is linked to improved water and nutrient retention. SOM is integral in ensuring soil integrity for water, air and nutrient recycling, which is fundamental for plant performance and yield production. High SOM content is usually found in loam and clayey soils, which also tend to support high WUE as previously alluded to.

2.4.5 *The relationships among environmental factors and WUE*

The positive correlations exhibited between N and WUE for all crops show that nitrogen availability is essential for plant growth and grain production. Nitrogen is an integral component of chlorophyll, the pigment that is responsible for light absorption to drive photosynthesis in higher plants. Therefore, its availability in the soil promotes photosynthesis, which results in higher grain production and WUE. Plants grown in N deficient soils suffer from chlorosis, which is the turning yellow of leaves, and their growth and productivity may be severely affected depending on the extent of deficiency, growth stage and genotype (Mu and Chen, 2021). As a result of low nutrient availability, organic and inorganic fertilisers are routinely applied to rectify nitrogen (N), potassium (K), phosphorous (P) and occasionally calcium (Ca), magnesium (Mg) and boron (Bo) deficiencies in agricultural soils to boost crop productivity. The Agricultural Green Revolution, which saw significant improvement in crop productivity per unit of land, was inspired by improvement in plant genetics and supported by availability of inorganic fertilisers to boost plant nutrient supply (Cassman and Grassini, 2013; Baum *et al.*, 2015). However, most farmers in SSA do not afford inorganic fertilizers. Suboptimal rates of fertilizer application are commonly used by farmers in this region. The per capita fertilizer use in SSA is 5.9 kg compared to 114.0 kg for the Oceania, 62.9 kg (North and Central America), 43.6 kg (South America), and 38.8 kg (Asia) (Zhang and Zhang, 2007). This has contributed to the low yields attained in SSA compared to other parts of the world. Also, nutrient deficiencies and sub-optimal fertilizer applications promote soil organic matter decomposition during nutrient mining by plants leading to soil degradation and greenhouse gas emissions (Chaplot, 2021). Modern crop varieties are efficient at nutrient mining and have yield potential in intensive agriculture systems but are susceptible in marginal environments. Therefore, it is important to identify crops and varieties that have high resource utilisation efficiency for designing appropriate production systems.

The negative association between MAP and WUE for maize and sorghum could be attributed to the fact that maize and sorghum are grown in summer season when temperatures are relatively higher than winter season in which wheat is normally grown. High water inputs through precipitation may not lead to high grain production. In modern agriculture systems, multiple cropping cycles are supported by irrigation to support crops grown outside of the normal rain season. Temperate crops such as wheat and barley are grown under irrigation during winter seasons in tropical environments (Cassman and Grassini, 2013). The low rainfall, temperatures and solar radiation during winter reduce evapotranspiration losses leading to high WUE although growth and development may be prolonged. For summer crops such as soybean and maize, irrigation mitigates recurrent and intermittent drought spells in environments characterised by low or uneven rainfall distribution. Summer seasons are characterised by high rainfall, temperatures and solar radiation, which increase evapotranspiration and reduce WUE in crops.

The summer season is also characterised by erratic rainfall, periodic drought spells and high evaporation rates, which reduce WUE (Rockström & Falkenmark, 2015). In summer, the thermal quotient is low due to the high evapotranspiration and high solar radiation. Thus, the provision of water through rainfall or irrigation is less effective at sustaining higher crop yields. The low thermal quotient in summer often linked to the high solar radiation that does not coincide with high mean precipitation (Cassman and Grassini, 2013) leading to poor water use efficiency. Similarly, high temperature increases evapotranspiration and reduce thermal quotient leading to low WUE. However, the combination of MAT and MAP is complex. There are ranges of MAT and MAP that are optimal for crop production and WUE usually increase from the low to the highest within the optimal range. Outside of the range, the WUE declines significantly as either MAT or MAP begins to interfere with biological processes. Temperature and rainfall must be sufficient for plant growth and within the optimal range for biomass production (e.g. Llorens *et al.*, 2003; Sánchez *et al.*, 2014).

Soil properties such as clay content, bulk density, pH, organic matter content, and organic carbon content exhibited positive correlations with WUE because, in general, increases in these parameters improve soil structure, fertility and water retention capacity, which promote good plant growth and productivity. Consequently, improved plant growth results in high WUE. For example, increase in clay content improves water and nutrient retention within the aggregates. However, when the clay content becomes too high crusting and cracking may occur with detrimental effects on root penetration for water and nutrients leading to crop failure. Organic carbon and matter contents of the soil are important for providing nutrients and allow microbial activity for plant growth.

The positive association between grain yield and WUE is important, particularly in marginal environments to convert the minimum available water into economic yield. Crops and varieties that have high WUE will produce more grain yield per unit of water available. The impact of environmental conditions on crop performance in biomass and grain yield production is affected by their pre-existing acclimation and photosynthetic pathway (Berry and Björkman, 1980). Thus, variation in biomass accumulation among the different crops point to their different acclimation, genetic constitution and potential, which govern their efficiency in utilizing water resources under the different water availability scenarios. In sorghum, the lack of association between WUE and grain yield could be attributed to lack of dynamic adaptation. The sorghum may have static adaptation, which is when a plant or genotype exhibits good or high grain production with minimal water resources but does not improve linearly with improved water availability. The association between WUE and grain yield is also influenced by differences in agronomic performance among hybrids, varieties and un-improved traditional varieties (Mbava *et al.*, 2020; Ficiciyan *et al.*, 2018; Lamptey *et al.*, 2014). Fang *et al.* (2014) reported higher WUE in modern improved varieties compared to old and un-improved landraces. Sorghum production is dominated by landraces and un-improved traditional varieties unlike maize and wheat, which receives far much greater attention in breeding programs for hybrid development and deployment. Therefore, the lack of association between WUE and grain yield could be due to the production of landraces that have static adaptation while maize and wheat hybrids experience dynamic adaptation. The multivariate analysis indicated that maize had the highest WUE and grain yield and received the highest amounts of water and fertiliser, which point to dynamic adaptation in response to water and nutrient availability.

2.5 Conclusions

Water use efficiency in maize, sorghum and wheat was analysed from 665 observations across the world. Maize was the most water use efficient crop followed by sorghum and wheat. The trend was supported by the difference in photosynthetic pathway and crop architecture. Maize and sorghum had higher WUE than wheat because they have the C4 photosynthetic system, which is more efficient than the C3 in wheat. However, the WUE changed under drought and nutrient stressed conditions. The WUE in maize declined in water and nutrient limited conditions showing that maize is more sensitive to resource availability. WUE increased in warmer and drier regions of the world with Africa and South America having higher average WUE than Europe and Asia. Increase in soil clay content, pH, bulk density, organic matter and carbon contents improved WUE. Among the crops, varietal differences in maize, sorghum and wheat were found to exist showing that WUE is determined by genotype. The complex interactions among the different environmental factors such as MAT and MAP, soil properties such as pH, soil texture and organic matter content and plant factors are difficult to elucidate in a single study. Therefore, the information generated from this study using data from multiple studies across the world provides essential foundation for understanding factors controlling WUE.

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CHAPTER 3: Crop genotype impact on biomass allocation and carbon storage: a meta-analysis on maize, sorghum, and wheat

Abstract

Crops store large amount of carbon (C), with part of it directly allocated belowground for direct input to the soil, thus directly providing food for the soil fauna and with enormous benefits for soil quality. While studies have quantified the differences in below-ground C storage between crop types, little is known about the variation between their cultivars, a valuable information for genetic screening. Hence, the objective of this study was to quantify the level of variation in biomass allocation and C storage in maize, sorghum, and wheat cultivars. Forty studies worldwide reporting on allocation of plant biomass and C between roots and shoots and for selected cultivars were used in this analysis. For each of them we assessed the variability between the cultivars by computing the standard deviations for total plant biomass and carbon stocks (Pb and Pcs, respectively), shoot (Sb, Scs), root (Rb, Rcs), root to shoot ratios (Rb/Sb; Rcs/Scs). Factors such as climate and soil management practices were also extracted from the articles to assess their effects in causing variability in biomass and C allocation between cultivars. Maize exhibited the highest Pb variability (31.2% of the mean Pb, with a standard deviation of ±11.4%; or 4.2±1.49 Mg ha^{-1} yr^{-1}), followed by wheat (24.2% or 1.5±0.4 Mg ha^{-1} yr^{-1}) and sorghum (16.8% or 2.0±0.8 Mg ha^{-1}). The same trend was observed for Rb, with maize (51.9% or 1.3 ± 0.6 Mg ha^{-1} yr^{-1}) followed by wheat (29.9% or 0. ±0.1 Mg ha^{-1} yr^{-1}), and sorghum (13.6% or 0.3 ± 0.2 Mg ha^{-1} yr^{-1}). A similar ranking between crop types was also observed for Rb/Sb (24.4%, 21.1% and 16.8%); Pcs (40.1%, 24.4%, and 16.3%). Scs (30.8%, 23.1%, and 17.0%), and Rcs (50.4% 30.9% and 16.8%). In contrast, wheat exhibited the highest variability for Rcs/Scs (30.9%) followed by maize (22.0%) and sorghum (16.8). The variability in Pb and Sb significantly decreased with increasing mean annual temperature (r = -0.47 and -0.43, respectively) and precipitation (-0.34; -0.30), while Rb variability increased (0.72; 0.85). The within-crop variability of all variables decreased with the increase in soil clay content and tillage increased the variability in all cases except for shoot and plant biomass and C stocks. This study provides evidence of high variability in carbon storage and biomass allocation within cereal cultivars, and we could identify the best cultivars and develop new ones that may be directly used by farmers to contribute to land rehabilitation and climate change mitigation. Overall, based on total biomass and carbon storage variations observed for root and shoot

carbon stocks between cereal cultivars, higher gains in carbon storage may be achieved by targeting maize and wheat for breeding rather than sorghum.

Keywords: Carbon stocks; biomass; C sequestration; cereals; variability

3.1 Introduction

Soils constitute the greatest terrestrial pool of carbon (C) and store two to three times the C that is found in the atmosphere (Minasny *et al.*, 2017). The amount of soil carbon has an influence on the quality, structure and water-holding capacity of soils which is critical for sustainable food production. Soil carbon, which is found as part of organic matter (OM) within the soil, is key for ecosystem functioning and provides a source of energy and nutrients for soil micro-organisms. However, due to the conversion of natural ecosystems to agricultural production, most of the original soil C has been lost to the atmosphere (Chaplot and Smith, 2023). According to Abbas *et al.* (2020), between 20 Mg C ha^{-1} and 50 Mg C ha^{-1} is lost within five and 50 years in tropical and temperate regions respectively due to land conversions to agriculture and land mismanagement. Therefore, putting C back into soils appears to be a credible strategy to rehabilitate degraded croplands and to reduce the carbon build up in the atmosphere (Daba and Dejene, 2018).

The atmosphere-plant-soil system is the most crucial part of the global C cycle with about 17% of the 720 Gt atmospheric C stock flowing through it each year (Jaradat, 2013). The assumption is that increasing soil C stocks would only require a slight increase in the flux of C from the atmosphere to plants and from plants to soils (Mathew *et al.*, 2017). Indeed, plants capture atmospheric C through photosynthesis for building their body and release organic carbon (OC) into the soil through rhizodeposition and decomposition of plant residues such as leaves, stems and roots (Abbas *et al.*, 2020). Furthermore, Balesdent and Balabane (1996) indicated that most of the C released into the soil by plants comes from roots rather than shoots and evidence from previous studies (Katterer *et al.*, 2011; Cardinael *et al.*, 2018; Hirte *et al.*, 2021) show that crops with higher root to shoot ratios (R/S) have up to 20% higher capacity to sequester carbon than crops with low R:S. Furthermore, Lorenz and Lal (2014) observed that root-derived soil organic carbon is 1.5 to 3.0 times higher than shoot-derived carbon. Roots are physically embedded in the soil, providing them with a more stable and secure environment. Soil provides a buffer against environmental factors such as temperature fluctuations, moisture changes, and exposure to light, which can increase the decomposition of organic matter (Buytaert *et al.*, 2011). The soil provides a shield that helps preserve root carbon for a longer period (Kramer *et al.*, 2012).

Variation in total biomass and C allocation between roots and shoots has been observed among crop types in several studies (Gonzalez-Sanchez *et al.*, 2012). In a global meta-analysis, Mathew *et al.* (2017) confirmed that maize had 11 and 32% higher shoot biomass and shoot C stocks compared to sorghum and wheat, respectively. Conversely, in Canada, Thivierge *et al.* (2016) reported higher shoot biomass for sorghum (19 kg ha^{-1}) followed by maize (17.6 kg ha^{-1}) and pearl millet (13.40 kg ha^{-1}). However, crop growth environments as affected by soil type, climate and management practices also exhibit significant effects on biomass and C allocation. For instance, in India, Kukal and Benbi, (2009) reported that wheat allocated 55% C to shoots in manure fertilized soils but allocated 45% C to the shoots in soils applied with chemical fertilisers. Similarly, Amujoyegbe *et al.* (2007) also reported an increase in root biomass and root carbon stocks allocation in maize by 35% and 18.2% in sorghum in Nigeria when N application rate was increased. This information can be used to match crop types to land and inform on the best management practices to adopt to increase biomass allocation to the roots for land rehabilitation and climate change mitigation. Not only do carbon allocation into crops differ between crop types but also between cultivars of single crops. Aquino *et al.* (2017) pointed out in Brazil, that the accumulation of carbon to maize shoots was 46% higher in a newly developed genotype “USM Var 10” than in “Crystal”, which is the local variety.

Currently, the knowledge of how different cereal crop varieties store carbon is presently limited with small variations of biomass allocation observed for different varieties (Xu *et al.*, 2020). Understanding the terrestrial C cycle requires measuring soil C input by crop genotypes. However, the fundamental genetic factors, processes involved in C sequestration, and how plant breeding programs can promote C sequestration remain poorly understood (Wegener *et al.*, 2015). Combining data from diverse research worldwide would allow a comparison of how carbon is allocated to shoots and roots of different cereal cultivars. Hence, the objective of this paper is to integrate results from different reports worldwide to assess variation in plant biomass and C allocation of maize, sorghum, and wheat cultivars, using data from individual sites. This information will provide information and guide breeders to develop plants with deeper and large roots to increase carbon deposition into the soil (Shamuyarira *et al.*, 2022).

3.2 Methods and materials

3.2.1 Study setup

Research articles published between 1980 and 2022, and reporting on plant biomass and carbon variables for shoots and roots were identified using Google Scholar, Scopus, and Web of Science. Keywords used to identify relevant articles were "carbon partition", "carbon allocation", "plant carbon sequestration", "root: shoot biomass carbon", "rhizodeposition", "plant/soil organic C stocks", "root and shoot carbon", "cereal", "maize", "sorghum" and "wheat". All relevant articles were entered into a Microsoft Excel database. Articles included in the database had to meet the following criteria: i) they had to report on plant (both root and shoot) biomass, C stocks and C content variables, ii) they had to report on data for either maize, sorghum or wheat cultivars, and iii) they had to report on experiments conducted in the field rather than in pots or controlled environments. For articles reporting on multi-year experiments, each year was treated as a separate and independent experiment, while in the case of replicated values, a mean was calculated for each treatment to avoid duplication and bias. The final database (summarized in Table 3.1) consisted of 509 datapoints from 40 research articles, reporting on 133 cultivars of maize, sorghum, and wheat. Nine main variables, namely plant biomass (Pb), shoot biomass (Sb), root biomass (Rb), total plant carbon content (Pcc), shoot carbon content (Scc), root carbon (Rcc) content, total plant carbon stocks (Pcs), shoot carbon stocks (Scs), and root carbon stocks (Rcs) were included in the final database. The observations in the final database were stratified using long-term climate variables (mean annual precipitation (MAP) and mean annual temperature (MAT)) and soil parameters (pH and texture,). When climatic variables were not explicitly reported in individual articles, they were retrieved from climate-data.org (2021) for the location where the experiment was conducted. The soil texture was cited from journal articles or determined using a soil texture triangle according to Mutema *et al.* (2015) when proportions of sand, silt and clay were reported. The soil pH derived from the research articles were converted using the CaCl2 scale and averaged across the soil profile to allow comparison using standardized values between research articles.

Table 3.1**:** References included in database with locations, crops and climatic zones under which the studies were conducted.

Paper ID	Author and year	Crop	No. of Cultivars	Country	Climate	Tillage
1	Amujoyegbe *et al.,* 2007	Maize, sorghum	2	Nigeria	Sub-tropical	No tillage
2	Anderson, 1988	Maize	1	USA	Temperate	Conventional, minimum tillage, no tillage
3	Aquino *et al.,* 2017	Maize	2	Philippines	Tropical	Conventional
4	Bolinder *et al.,* 1997	Wheat	8	Canada	Temperate	Conventional
5	Christiansen-Weniger *et al.,* 1992	Wheat	3	Netherlands	Tropical	Conventional
6	Comin *et al.,* 1999	Maize	2	Brazil	Tropical	Conventional
7	Das *et al.,* 2016	Maize, Sorghum	2	USA	Temperate	No tillage
8	Figueroa-Bustos *et al.,* 2018	Wheat	5	Australia	Tropical	Conventional
9	Gan *et al.*, 2009	Wheat	1	Canada	Temperate	Conventional
10	Geng *et al.,* 2006	Wheat	2	China	Sub-tropical	Conventional
11	Hebert *et al.,* 2001	Maize	7	France	Temperate	Conventional
12	Hussein and Alva, 2014	Sorghum	1	Egypt	Tropical	Conventional
13	Mathew *et al.,* 2019	Wheat	15	South Africa	Temperate	Conventional
14	Kanchikerimath and Singh, 2001	Maize	1	India	Sub-tropical	Conventional
15	Kaushik *et al.,* 2005	Wheat	3	India	Tropical	Conventional
16	Khorramdel *et al.,* 2013	Maize	1	Iran	sub-tropical	Conventional
17	Kundu *et al.,* 2007	Wheat	1	India	Sub-tropical	Conventional
18	Liang *et al.,* 2020	Maize	2	China	Temperate	Conventional
19	Liu *et al.,* 2014	Maize	4	China	Temperate	No tillage
20	Martin and Kemp, 1980	Wheat	12	Australia	Temperate	Conventional
21	Meki *et al.,* 2013	Sorghum	1	USA	Tropical	Conventional, minimum

Paper ID	Author and year	Crop	No. of Cultivars	Country	Climate	Tillage
						tillage, no tillage
22	Meskelu *et al.,* 2014	Maize	1	Ethiopia	Sub-tropical	Conventional
23	Montanez *et al.,* 2012	Maize	2	Uruguay	Temperate	Conventional
24	Msongaleli *et al.,* 2017	Sorghum	3	Tanzania	Tropical	Minimum tillage
25	Nguyen *et al.,* 2019	Wheat	2	Australia	Tropical	Conventional
26	Promkhambut *et al.,* 2010	Sorghum	4	United Kingdom	Tropical	Conventional
27	Sainju *et al.,* 2005	Sorghum	1	USA	Temperate	No tillage
28	Schortemeyer *et al.,* 1997	Maize	4	USA	Tropical	Conventional, minimum tillage
29	Shaheen and Hood-Nowotny, 2005	Wheat	4	Austria	Sub-tropical	Conventional
30	Shen *et al.,* 2007	Wheat	1	China	Temperate	No tillage
31	Srinivasarao *et al.,* 2012	Sorghum	1	India	Sub-tropical	Conventional
32	Teravest *et al.,* 2015	Maize	1	Malawi	Tropical	No tillage
33	Thivierge *et al.,* 2016	Maize, sorghum	2	Canada	Temperate	Minimum tillage
34	Van de Broek *et al.,* 2020	Wheat	4	Switzerland	Tropical	Conventional
35	Wang *et al.,* 2007	Wheat	3	China	Sub-tropical	Conventional
36	Wang *et al.,* 2018	Maize	5	China	Temperate	No tillage
37	Xia *et al.,* 2021	Maize	2	China	Temperate	Conventional
38	Xu *et al.,* 2019	Maize	10	Belgium	Temperate	Conventional
39	Xu *et al.,* 2020	Maize	10	Belgium	Temperate	Conventional
40	Zan *et al.,* 2001	Maize	1	Canada	Temperate	Conventional

3.2.2 *Biomass and C allocation variables*

Definitions for Pb, Rb, Sb, Rb/Sb, Pcc, Scc, Rcc, Pcs, Scs, Rcs, and Rcs/Scs are summarized in Table 3.2. Soil properties (clay content, bulk density and pH) are also described on Table 3.3. All the definitions used in the current study were exclusively for the purposes of the current analysis and are not intended to be used in other contexts. These definitions matched the majority of the studies, except for a few studies where the authors did not separate roots from shoots. For the purposes of this study, all biomass was considered as shoot biomass when no distinction was made between roots and shoots. In articles where plant biomass and plant carbon variables were not provided, they were derived from adding shoot and root variables for biomass and carbon respectively. In instances were plant biomass, C stocks and C content variables were not reported directly, estimates were obtained using harvest indices and root-to-shoot ratios reported in the experiment. Where the biomass and carbon variables were not explicitly stated in the paper, they were estimated using ratios according to the following formulae:

$$Rb = Rb{:}Sb \times Sb \quad (1)$$

$$Sb = Rb{:}Sb \times Rb \quad (2)$$

$$Pb = Sb + Rb \quad (3)$$

$$Pcc = Pcs/Pb \times 100 \quad (4)$$

$$Scc = Scs/Sb \times 100 \quad (5)$$

$$Rcc = Rcs/Sb \times 100 \quad (6)$$

Also, where the carbon variables were not stated, they were estimated according to Bar-On *et al.* (2018) using the following formulae:

$$Scs = Sb \times Scc \quad (7)$$

$$Rcs = Rb \times Rcc \quad (8)$$

$$Pcs = Scs + Rcs \quad (9)$$

Where Rb is the root biomass (Mg ha^{-1}), Sb the shoot biomass (Mg ha^{-1}), Pb the total plant biomass (Mg ha^{-1}), Rb/Sb the root to shoot biomass ratio, Rcc the root carbon content (%), Scc the shoot carbon content (%), Pcc the total plant carbon content (%), Scs the shoot carbon stock

(Mg C ha^{-1}), Rcs the root carbon stock (Mg C ha^{-1}), and Pcs the total plant carbon stock (Mg c ha^{-1}).

Table 3.2: Descriptions of biomass and carbon variables used in this study.

Variable	Symbol	Unit	Definition
Plant biomass	Pb	Mg ha^{-1}	The total mass of root and shoot biomass of the crop.
Root biomass	Sb	Mg ha^{-1}	The mass of above-ground biomass (stems and leaves) of the crop.
Shoot biomass	Rb	Mg ha^{-1}	The mass of below ground biomass of the crop, excluding harvestable components.
Plant carbon content	Pcc	%	The total concentration of carbon in the roots and shoots.
Shoot carbon content	Scc	%	Concentration of carbon in the shoots.
Root carbon content	Rcc	%	Concentration of carbon in the roots.
Plant carbon stock	Pcs	Mg C ha^{-1}	The total quantity of carbon contained in the entire plant, as stated by the authors, or as the sum of root and shoot carbon stocks.
Shoot carbon stock	Scs	Mg C ha^{-1}	The total quantity of carbon in the shoot biomass as stated by the authors or calculated as shoot biomass multiplied by shoot carbon concentration.
Root carbon stock	Rcs	Mg C ha^{-1}	The total quantity of carbon in the root biomass stated by authors or calculated as root biomass multiplied by root carbon concentration.
Root:shoot ratio of biomass	Rb/Sb		An expression of root biomass as a fraction of shoot biomass.
Root:shoot ratio of carbon stock	Rcs/Scs		An expression of root carbon stocks as a fraction of shoot carbon stocks.

Table 3.3: Environmental factors and their factor classes

Factor	Remarks	Categories	Symbol	Factor class
Soil pH	Soil pH as reported in the article	< 5.5 6.5-7.5 > 7.5	pH	Acidic Neutral Alkaline
Soil bulk density (g cm^{-3})	Average bulk density (BD) of soil profile	< 1.5 > 1.5	BD	Low High
Fertilizer application	Amount of fertilizer applied on the soil, as cited on the paper	N (kg/ha) P as P_2O_5 (kg/ha) K as K_2O (kg/ha)	NPK	Applied Nitrogen Applied Phosphate fertilizer. Potassium applied.
Climatic region	Based on the study site's average annual temperature and precipitation	Precipitation > 1000 mm Temperature > 20°C Precipitation 300-1000 mm Temperature 10-20 Precipitation < 800 mm Temperature < 10°C	Hot and warm Warm and arid humid Cool and arid to moist	Tropical Sub-tropical Temperate

Factor	Remarks	Categories	Symbol	Factor class
Soil texture	Soil texture based as cited on the paper or based on soil texture triangle	% Clay % Silt % Sand	Texture	Clay, Sand, Loam, Sandy clay, Sandy clay loam, loamy sand, clay loam, silt loam, etc.
Tillage	The mechanical manipulation of the soil for the goal of crop production.	No ploughing at all Targeted ploughing Deep ploughing	Tillage	No-tillage. Minimum Conventional
Mulching	Covering of soil between plants with a layer of material (plastic)	Soil mulch Plastic mulch Organic mulch	Mulch	No mulch Half mulch Full mulch

3.2.3 *Variability of biomass and carbon variables*

Standard deviations for all biomass and carbon variables were calculated per individual site for each crop to determine the variation among cultivars at different sites. Standard deviations were calculated as measure of variability between maize, sorghum, and wheat cultivars in Pb, Sb, Rb, Rb/Sb, Pcc, Scc, Rcc, Pcs, Scs, Rcs, and Rcs/Scs.

3.2.4 Data analyses

Standard deviations were calculated in Microsoft Excel 2016 for each paper as a measure of the variability of cultivars in that location. Summary statistics were generated for standard deviations of biomass allocation, C content, and C stocks using Genstat 18th edition (Payne *et al.*, 2017), which were outlined by mean, median, minimum, maximum, first quartile (Q1) and third quartile (Q3), standard deviation (SD), coefficient of variation (CV), skewness, and kurtosis. Box plots were used to demonstrate the variability of datasets based on standard deviations obtained per individual site for the three crop types. Each boxplot recorded the outliers, minimum, maximum, median, mean, Q1 and Q3 values. Bar graphs showing the variability between crop cultivars expressed in percent of mean total biomass, C content, and C stocks were generated using Microsoft Excel 2016. Correlation coefficients (r), based on Spearman Rank correlations, were carried out using IBM SPSS statistics (Wagner, 2019) to determine the strength of associations between variables. A multivariate analysis, using uncentred principal component analysis (PCA) was conducted using R statistical software (R Core Team, 2022) to show the multiple relationships of the variation for biomass allocation, C allocation and C content with environmental factors. Each variety was given a number to identify it in the PCA biplot.

3.3 Results

3.3.1 *Variation of plant biomass, carbon content, and C stocks of cereal cultivars*

The variabilities for biomass, carbon content, and C stocks recorded at individual sites of maize, sorghum, and wheat are summarized in Table 3.4. Maize (4.18 Mg ha^{-1}) accumulated the highest mean variability in plant biomass (Pb), compared to sorghum (2.02 Mg ha^{-1}) and wheat (1.10 Mg ha^{-1}) (Table 3.4). All the crops showed a similar trend with regards to biomass and C allocation variability in shoots and roots; with shoots showing higher variability than roots across crop types (Figure 3.1a and 3.1c). Wheat had the lowest variability in shoot biomass (Sb) than sorghum and maize, but higher variability in root biomass (Rb) compared to sorghum, with mean variability in Sb and Rb of 1.11 Mg ha^{-1} and 0.51 Mg ha^{-1}, respectively. Maize showed great variability across plant and shoot variables, whereas sorghum showed more variability when compared to wheat. Wheat had the highest mean (0.13) variability in root to shoot biomass ratio (Rb/Sb), followed by maize (0.07), then sorghum (0.04).

Table 3.4**:** Summary statistics of biomass variables for maize, sorghum and wheat

Statistics	Pb			Sb			Rb			Rb/Sb		
	Maize	Sorghum	Wheat	Maize	Sorghum	Wheat	Maize	Sorghum	Wheat	Maize	Sorghum	Wheat
No.	19	8	13	19	8	13	19	8	13	19	8	13
Mean	4.18	2.02	1.49	3.31	1.76	1.11	1.27	0.32	0.51	0.07	0.04	0.13
Median	1.51	0.85	1.22	1.43	0.68	0.87	0.38	0.13	0.40	0.02	0.04	0.10
Min.	0.06	0.04	0.11	0.04	0.03	0.06	0.02	0.01	0.04	0.00	0.001	0.03
Max.	20.48	6.73	6.48	14.47	5.34	3.85	11.03	1.39	1.86	0.57	0.25	0.44
Q1	0.91	0.49	0.49	0.67	0.25	0.35	0.14	0.04	0.26	0.001	0.02	0.04
Q3	4.56	3.08	1.84	4.40	3.05	1.68	0.85	0.30	0.60	0.08	0.10	0.18
SD	5.80	2.23	1.56	4.22	1.94	1.05	2.55	0.45	0.46	0.13	0.08	0.12
SEM	1.33	0.79	0.42	0.97	0.69	0.28	0.58	0.16	0.12	0.03	0.03	0.03
Variance	33.66	4.96	2.43	17.82	3.75	1.10	6.50	0.20	0.21	0.02	0.01	0.01
%CV	138.79	110.03	105.01	127.51	110.16	94.35	200.08	140.35	90.01	186.60	179.42	94.80
Skewness	2.03	1.08	2.19	1.81	0.82	1.23	3.06	1.63	1.75	3.22	1.90	1.13
Kurtosis	4.16	0.98	7.51	3.23	-0.64	1.73	11.71	3.99	4.79	13.66	5.81	1.63

No = number of values, N = number of observations, Min and Max = minimum and maximum, respectively, Q_1 and Q_3 = first and third quartile, respectively, SD = standard deviation, SEM = standard error of mean, SEV = Standard error of variance, and CV = coefficient of variation. See Table 2 for descriptions and units.

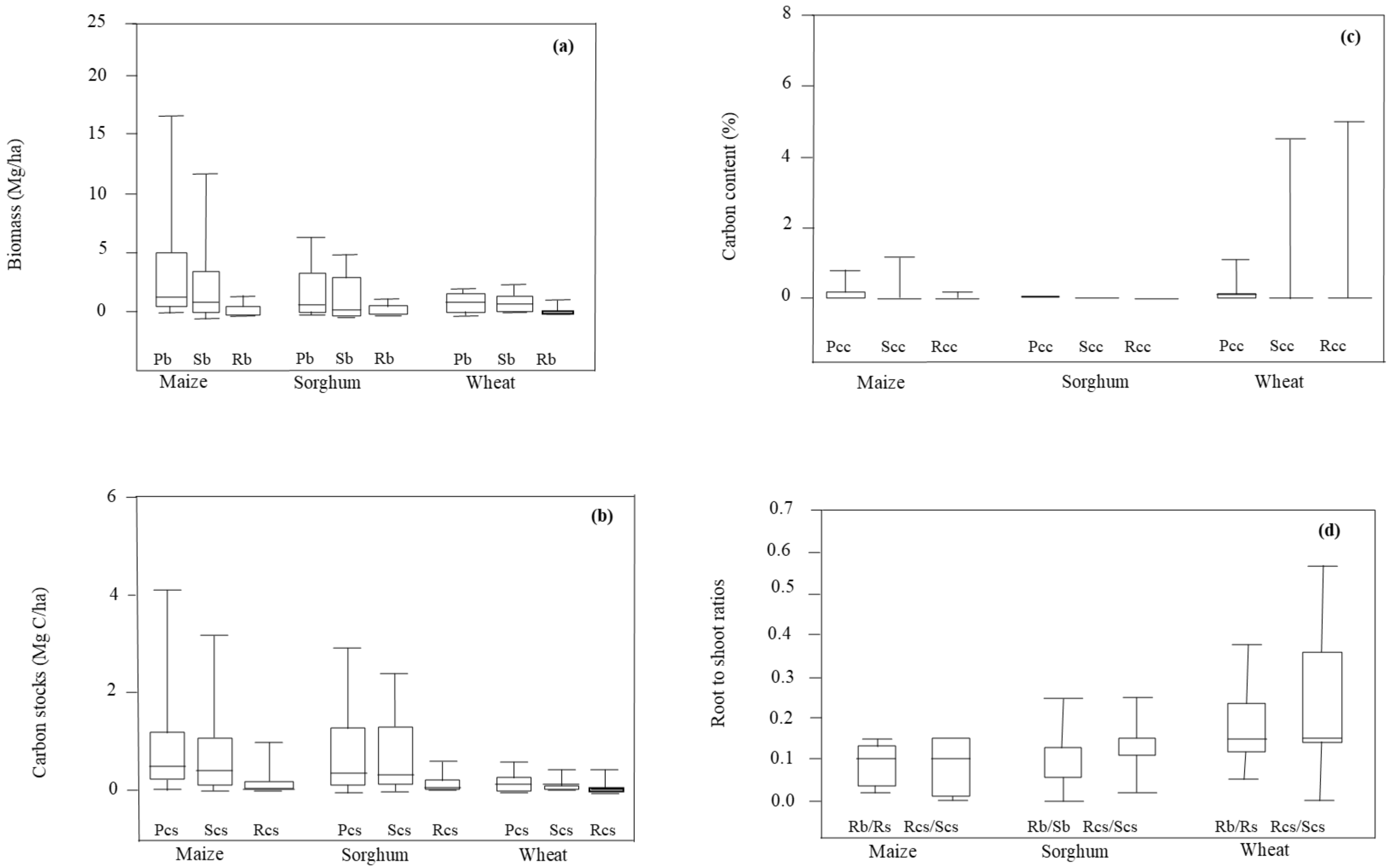

Figure 3.1: Variability between crop cultivars in total plant biomass (Pb), shoot biomass (Sb), and root biomass (Rb) (a); total plant carbon content (Pcc), shoot carbon content (Scc), and root carbon content (Rcc) (b); total plant carbon stock (Pcs), shoot carbon stock (Scs), and root carbon stock (Rcs) (c); root to shoot biomass ratio (Rb/Sb) and root to shoot carbon stocks ratio (Rcs/Scs) (d) of maize, sorghum, and wheat. Each box plot presents the minimum, maximum, median, quartile 1 (25%), and quartile 3 (75%).

Maize also had the highest variability for total plant carbon content (Pcc) with the maximum variability of 37.42% followed by wheat (6.63%) and sorghum (2.24%) (Table 3.5 and Figure 3.1b). Wheat had the highest variability in shoot carbon content (Scc) and sorghum had the highest variability in root carbon content (Rcc) with mean variability values of 0.58% and 0.64%, respectively. There is very low variation for carbon content between cultivars with constant variables recorded coefficient of variation (CV) and standard variation (SD).

Table 3.5**:** Summary statistics of carbon content variables for maize, sorghum and wheat

Statistics	Pcc			Scc			Rcc		
	Maize	Sorghum	Wheat	Maize	Sorghum	Wheat	Maize	Sorghum	Wheat
No.	19	8	13	19	8	13	19	8	13
Mean	2.30	0.52	0.95	0.10	0.30	0.58	0.12	1.19	0.64
Median	0.03	0.03	0.40	0.61	0.00	0.00	0.00	0.00	0.00
Min.	0.001	0.001	0.00	0.001	0.00	0.00	0.001	0.00	0.00
Max.	37.42	2.24	6.63	1.30	2.42	4.51	2.03	8.03	6.85
Q1	0.001	0.00	0.06	0.001	0.00	0.00	0.00	0.00	0.00
Q3	0.38	0.56	0.72	0.99	0.00	0.00	0.18	0.36	0.00
SD	8.32	0.84	1.68	0.32	0.80	1.43	0.45	2.63	1.81
SEM	1.91	0.30	0.45	0.07	0.28	0.38	0.30	0.93	0.48
Variance	69.24	0.71	2.83	0.10	0.64	2.04	0.21	6.93	3.27
%CV	361.86	161.96	177.88	307.62	264.57	246.73	388.74	222.00	281.94
Skewness	3.94	1.24	2.74	3.03	2.27	2.10	3.96	2.13	2.90
Kurtosis	18.54	0.79	10.06	10.86	8.00	4.33	18.63	7.20	10.97

No. = number of values, N = number of observations, Min and Max = minimum and maximum, respectively, Q_1 and Q_3 = first and third quartile, respectively, SD = standard deviation, SEM = standard error of mean, SEV = Standard error of variance, and CV = coefficient of variation. See Table 2 for descriptions and units.

Maize had the highest variability in total plant carbon stocks (Pcs) ranging from a minimum 0.02 Mg C ha^{-1} to 14.36 Mg C ha^{-1} with a mean variability value of 1.55 Mg C ha^{-1} followed by sorghum (0.83 Mg C ha^{-1}) (Table 3.6 and Figure 3.1d). The variability in root biomass and carbon stocks between were low across all crop types compared to variability in shoot parts. Wheat had the highest mean (0.18) variability in root to shoot carbon stock ratio (Rcs/Scs), followed by maize (0.06), then sorghum (0.05).

Table 3.6**:** Summary statistics of Carbon stocks variables for maize, sorghum and wheat

Statistics	Pcs			Scs			Rcs			Rcs/Scs		
	Maize	Sorghum	Wheat	Maize	Sorghum	Wheat	Maize	Sorghum	Wheat	Maize	Sorghum	Wheat
No.	19	8	13	19	8	13	19	8	13	19	8	13
Mean	1.55	0.85	0.21	0.82	0.73	0.12	0.29	0.16	0.11	0.06	0.05	0.18
Median	0.46	0.46	0.16	0.38	0.30	0.09	0.09	0.06	0.07	0.01	0.02	0.13
Min.	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.003	0.001	0.001	0.001	0.01
Max.	14.36	2.94	0.83	3.56	2.35	0.48	2.52	0.59	0.56	0.53	0.24	0.69
Q1	0.22	0.21	0.05	0.16	0.11	0.03	0.05	0.04	0.03	0.0002	0.00	0.01
Q3	1.22	1.25	0.27	1.08	1.24	0.12	0.19	0.27	0.12	0.07	0.05	0.29
SD	3.20	0.92	0.23	1.04	0.80	0.13	0.58	0.19	0.14	0.12	0.08	0.19
SEM	0.73	0.33	0.06	0.24	0.28	0.03	0.13	0.07	0.04	0.03	0.03	0.05
Variance	10.23	0.85	0.05	1.08	0.64	0.02	0.34	0.04	0.02	0.01	0.01	0.04
%CV	206.66	107.96	109.46	127.16	109.94	107.32	197.46	115.51	126.97	206.13	155.54	106.22
Skewness	3.39	1.26	1.55	1.80	0.94	1.60	3.07	1.24	2.48	3.26	1.83	1.24
Kurtosis	14.46	2.41	2.84	3.21	0.29	3.53	11.75	2.14	8.86	13.82	5.58	2.21

No. = number of values, N = number of observations, Min and Max = minimum and maximum, respectively, Q_1 and Q_3 = first and third quartile, respectively, SD = standard deviation, SEM = standard error of mean, SEV = Standard error of variance, and CV = coefficient of variation. See Table 2 for descriptions and units.

3.3.2 *Variability expressed in percent of mean biomass, C content, and C stocks*

The variability between cultivars expressed in percent of mean plant biomass, carbon content, and C stocks are presented on Figure 3.2 and Table 3.7. Maize and wheat had higher variability expressed in percent of mean Pb, Sb, and Rb (Figure 3.2a). Sorghum showed the lowest variability expressed in percent of mean Pb (16.82%), Sb (18.13%), and (36.96%), respectively compared to maize and wheat. The variability expressed in percent of mean Sb in maize and wheat was greater than 27.97% and was twice the variability expressed in percent of mean Sb in sorghum. Maize had variability expressed in percent of mean Pb exceeding 31.89% compared to 24.15% of wheat.

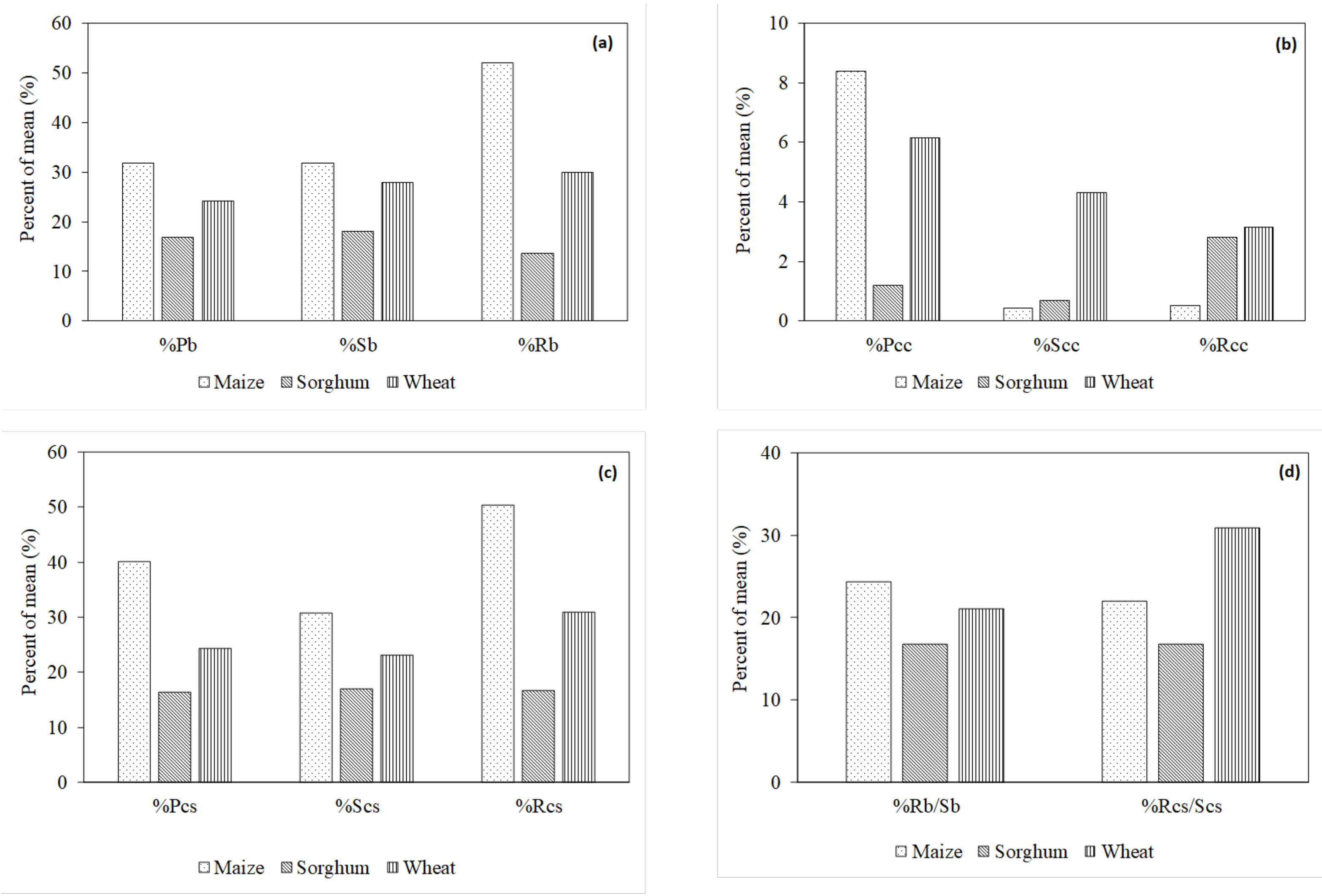

Figure 3.2**:** Variability between crop cultivars expressed in percent of mean total plant biomass (%Pb), shoot biomass (%Sb), and root biomass (%Rb) (a); total plant carbon content (%Pcc), shoot carbon content (%Scc), and root carbon content (%Rcc) (b); total plant carbon stock (%Pcs), shoot carbon stock (%Scs), and root carbon stock (%Rcs) (c); root to shoot biomass ratio (%Rb/Sb) and root to shoot carbon stocks ratio (%Rcs/Scs) (d) of maize, sorghum, and wheat. See Table 2 for descriptions and units.

Table 3.7: Mean variability and percent of mean variability for plant biomass and carbon stocks for maize, sorghum, and wheat.

Mean SD	Pb	Sb	Rb	Rb/Sb	Pcc	Scc	Rcc	Pcs	Scs	Rcs	Rcs/Scs
Maize	4.18	3.31	1.27	0.07	2.3	0.1	0.42	1.55	0.82	0.29	0.06
Sorghum	2.02	1.76	0.32	0.04	0.52	0.30	1.19	0.85	0.73	0.16	0.05
Wheat	1.49	1.11	0.51	0.13	0.95	0.58	0.64	0.21	0.12	0.11	0.18
SD of SD											
Maize	5.80	4.22	2.55	0.13	8.32	0.32	0.45	3.20	1.04	0.58	0.12
Sorghum	2.23	1.94	0.45	0.08	0.84	0.80	2.63	0.92	0.80	0.19	0.08
Wheat	1.56	1.05	0.46	0.12	1.68	1.43	1.81	0.23	0.13	0.14	0.19
SD expressed in percent of mean											
Maize	31.89	31.78	51.97	24.38	8.39	0.42	0.51	40.13	30.76	50.38	22.02
Sorghum	16.82	18.13	13.64	16.79	1.19	0.69	2.82	16.30	17.03	16.76	16.76
Wheat	24.15	27.97	29.94	21.09	6.15	4.32	3.15	24.35	23.14	30.92	30.92

See Table 2 for descriptions and units.

Similar trends were observed for carbon content variables with maize excelling higher than the other crops. Maize (8.39%) had the highest variability expressed in percent of mean Pcc, followed by wheat (6.15%), and sorghum (1.19%). Wheat had the highest variability expressed in percent of mean. Wheat amassed the highest variability expressed in percent of mean Scc and Rcc (4.32% and 3.15%, respectively), followed sorghum (0.69% and 2.82%, respectively) and maize (0.42% and 0.51%, respectively) (Figure 3.2b).

Maize exhibited higher variability expressed in percent of mean Pcs, Scs, and Rcs compared to sorghum and wheat with the values of 40.13%, 30.76%, and 50.38%, respectively. Sorghum had the lowest variability expressed in percent of mean carbon stocks for all variables measured (Figure 3.2c). Maize had the highest variability expressed in percent of mean Rb/Sb and wheat displayed the highest variability expressed in percent of mean Rcs/Scs with values of 24.38% and 30.92%, respectively (Figure 3.2d).

3.3.3 *Global variability expressed in percent of mean plant biomass, C content, and C stocks*

The variability between cultivars expressed in percent of mean plant biomass, C content, and C stocks for different continents are presented on Figure 3.3. Europe (Pb = 40.02%, Sb = 41.39%, and Rb = 70.74%) had the highest variability expressed in percent of mean biomass for all the biomass variables, followed by Africa (Pb = 35.46%, Sb = 35.81%, and Rb = 37.18%) and Asia (Pb = 31.18%, Sb = 33.9%, and Rb = 38.13%). The continents with the lowest variability expressed in percent of mean biomass for all the biomass variables were

South America, followed by North America, and Oceania (Figure 3.3a). Similar trends were observed for C content with Europe continuing to excel for variability expressed in percent of mean C content for all the C content variables (Figure 3.3b).

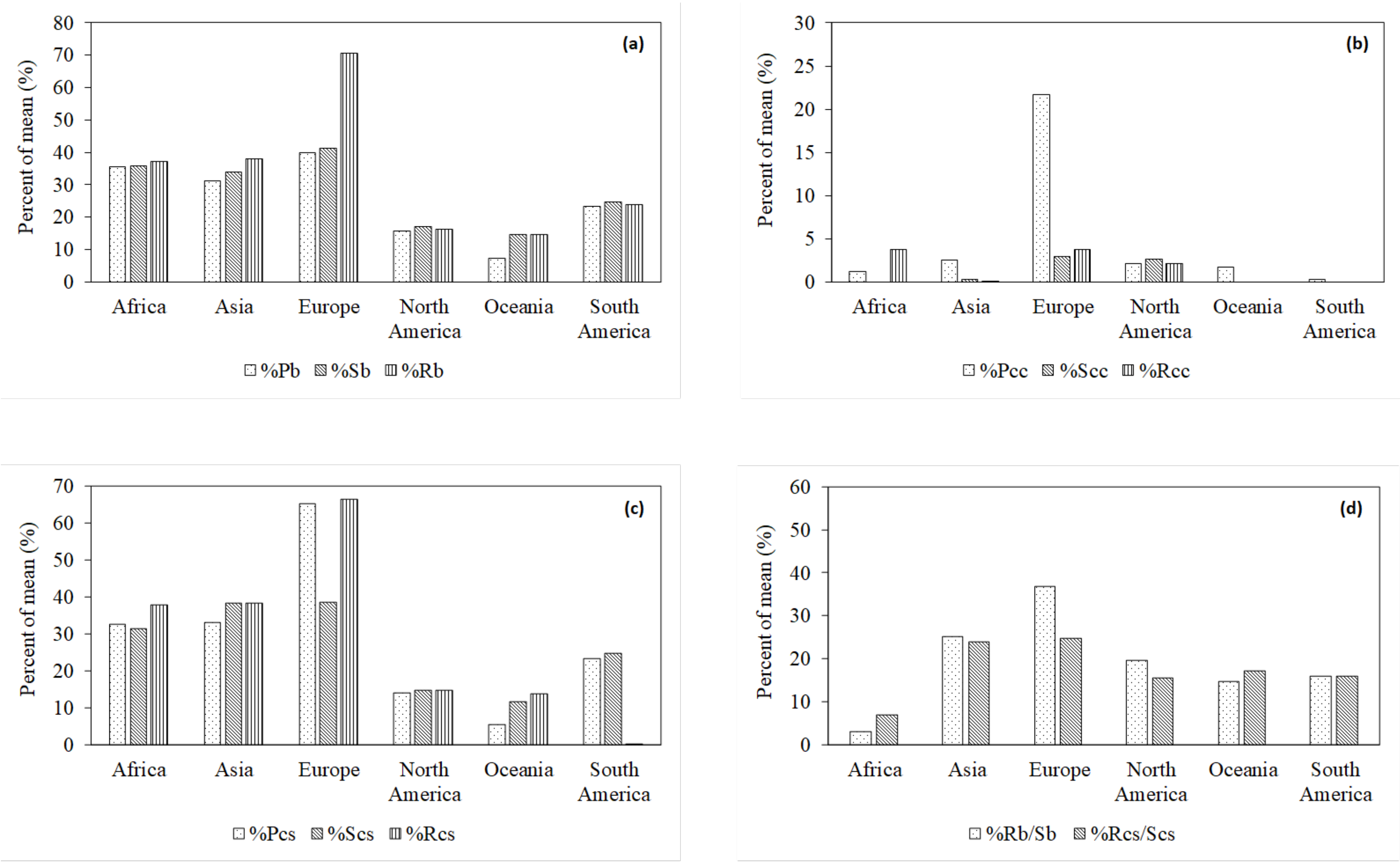

Figure 3.3:Variability between crop cultivars expressed in percent of mean total plant biomass (%Pb), shoot biomass (%Sb), and root biomass (%Rb) (a); total plant carbon content (%Pcc), shoot carbon content (%Scc), and root carbon content (%Rcc) (b); total plant carbon stock (%Pcs), shoot carbon stock (%Scs), and root carbon stock (%Rcs) (c); root to shoot biomass ratio (%Rb/Sb) and root to shoot carbon stocks ratio (%Rcs/Scs) (d) of maize, sorghum, and wheat for different continents. See Table 2 for descriptions and units.

Europe (Pcs = 65.13%, Scs = 38.55%, and Rcs = 66.22%) continued to have the highest variability expressed in percent of mean C stocks for all the carbon variables, followed by Asia (Pcs = 33.00%, Scs = 38.19%, and Rcs = 38.31%), and Africa (Pcs = 32.46%, Scs = 31.34%, and Rcs = 37.82%) (Figure 3.3c). Europe exhibited the highest variability expressed in percent of mean Rb/Sb and Rcs/Scs (36.73% and 24.84%, respectively) (Figure 3.3d).

3.3.4 *Associations between environmental factors and variabilities for biomass, C stocks, and carbon content*

Mean annual precipitation and variability in Rb displayed the strongest significant positive correlation ($r = 0.85$, $p < 0.05$) suggesting a direct link between the two (Table 3.8). The variability in Pb and Sb had a significantly negative correlation with all the environmental factors (MAP, MAT, clay and tillage). The variability in Pcs and Scs followed the same trend but showing an insignificant correlation. Mean annual temperature had the strongest significant positive correlation ($r = 0.72$, $p < 0.05$) with variability in Rb. Clay showed negative associations with all the plant variables. Mean annual precipitation exhibited the strongest correlations with variability in Rb/Sb and Rcs/Scs ($r = 0.80$ and $r = 0.80$, $p < 0.05$, respectively) compared to MAT and tillage. This trend was the same with variability in Rcs. Tillage and variability in Rb, Rb/Sb, and Rcs/Scs exhibited the strongest significant correlation ($r = 0.61$, $r = 0.55$, and $r = 0.53$, $p < 0.05$, respectively). The variability in Pcc, Scc, and Rcc exhibited non-significant correlations will all the environmental factors.

Table 3.8**:** Correlations displaying relationship between biomass, C stocks, carbon content, and environmental factors for maize, sorghum, and wheat.

Plant variables	MAT	MAP	Clay	Tillage
Pb	-0.47*	-0.34*	-0.73*	-0.55*
Sb	-0.43*	-0.30*	-0.70*	-0.51*
Rb	0.72*	0.85*	-0.29	0.61*
Rb/Sb	0.67	0.81*	-0.36	0.55*
Pcc	0.58	0.73	-0.45	0.45
Scc	0.39	0.57	-0.61	0.25
Rcc	0.49	0.66	-0.56	0.35
Pcs	-0.45	-0.31	-0.76	-0.54
Scs	-0.70	-0.63	-0.54	-0.73
Rcs	0.60	0.76	-0.44	0.48
Rcs/Scs	0.65	0.80*	-0.38	0.53*

* Significance at $P \leq 0.05$. See Table 2 for descriptions and units.

3.3.5 *Multivariate analysis for variability of biomass and C allocation*

A biplot based on the principal component analysis (PCA) of variables reflecting the variation of biomass, carbon stock and carbon content of different cereals is shown in Figure 3.4. The first and second principal components (PC1 and PC2) accounted for a total variation of 79.6% with PC1 accounting for 60.4% of the variation while PC2 accounted for only 19.4%. The variability between cultivars in Rcs, Pcs, and Rb were strongly correlated with PC1. On the other hand, PC2 was positively correlated with the variability in Scc and Rcc. Maize varieties were correlated to PC1, while wheat varieties contributed more to PC2. Maize variety 13 excelled in variability Scs, while wheat variety 40 scored highly for variability in Rcc. Only sorghum variety 25 performed differently from other sorghum varieties with high correlations with variability in Sb and Scs.

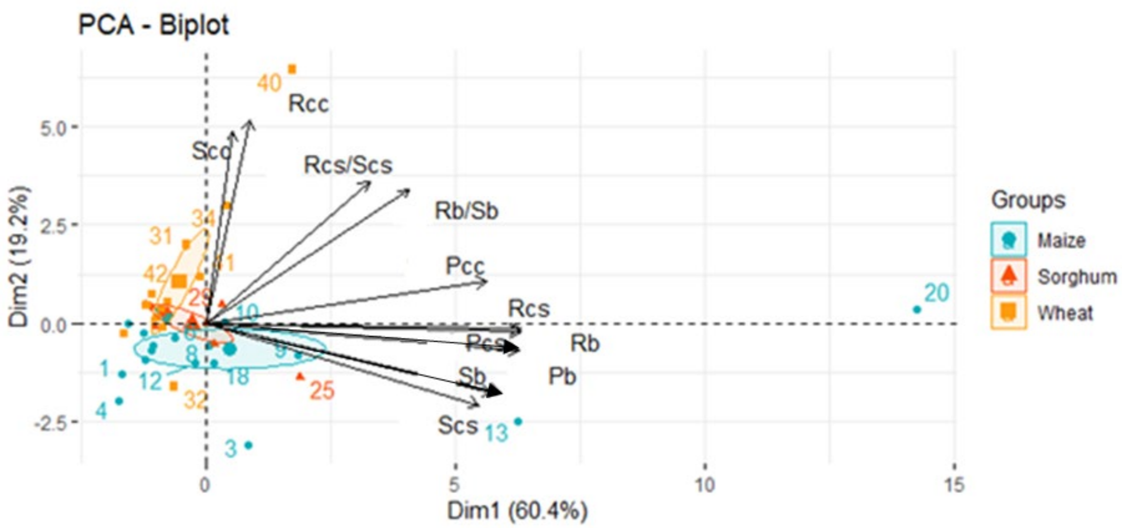

Figure 3.4: Principal component biplot of variability in plant biomass, C content, C stocks between cultivars of maize, sorghum, and wheat. See Table 2 for descriptions and units.

In Figure 3.5, the first PC explains 60.4% of the variability and correlates with the variability in Pb and Pcs and could thus be interpreted as an axis of variableness in biomass production and carbon accumulation. The second PC explains 19% of data variability and is correlated with the variability in Rcc and Scc and could thus be interpreted as an axis of carbon enrichment. Maize shows a positive coordinate on PC1 and a negative one on PC 2.

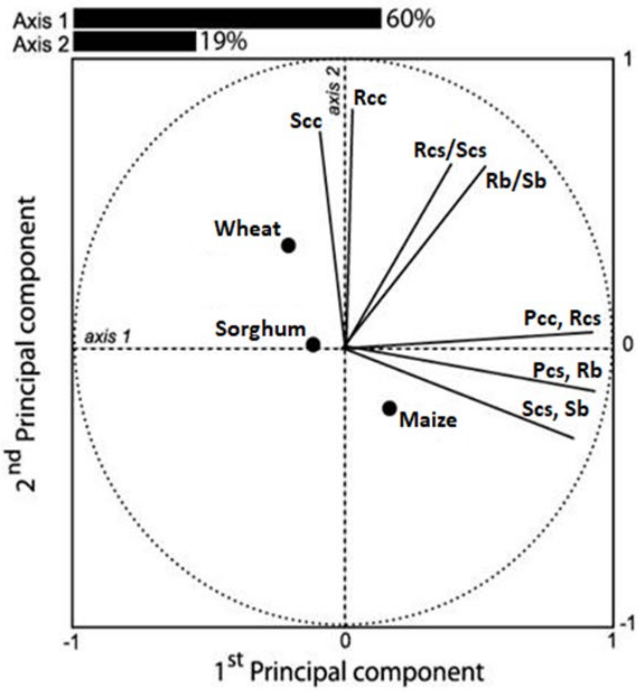

Figure 3.5: Principal Component Analysis (PCA) between maize, sorghum, and wheat as variables for analysis and variability in plant biomass, C content, and C stocks as supplementary variables. See Table 2 for descriptions and units.

A PCA was generated using selected variables of the environment (Figure 3.6). The first axis explained 43% of the variability in the data while the second axis explained 29% of the variation. The first axis correlated with soil clay content and MAP, and the second axis was closely correlated with MAT and intensity of soil tillage on the negative coordinates. Several study variables including variability Rb/Sb and Rcs/Scs showed negative coordinates on Axis 2. On the other hand, variability in Pb, Sb, and carbon stocks between cultivars increased as MAT decreases and as tillage intensity decreases.

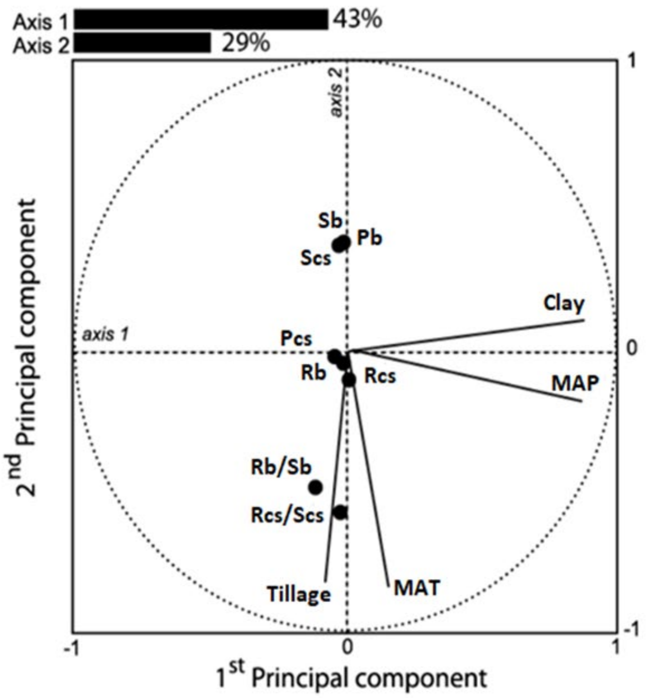

Figure 3.6: PCA displaying associations between variability in plant biomass, C variables, and environmental parameters. See Tables 2 and 3 for descriptions and units.

3.4 Discussion

3.4.1 *Causes of variation in biomass allocation amongst crop types*

This current study shows that different crop types exhibited significant variations in biomass allocation as shown by Monte *et al.* (2008) (Table 3.5). A higher amount of biomass was measured in maize compared to sorghum and wheat for all the plant variables which is consistent with Ritchie *et al.* (1998) and Guzman and Al-kaisi (2010). In comparison to other cereals, maize produces more biomass because it maximizes light absorption for the synthesis of carbon assimilates that are used to drive biomass production (Stewart and Amanullah, 2013). Investments for maize improvement have been largely directed to several breeding programs around the world focusing on improving traditional maize landraces and developing improved open-pollinated varieties (OPV) or hybrid varieties from them. The result of maize improvement has thus been increased yield. As a cross-pollinating crop, maize has higher hybrid vigor compared to sorghum or wheat, and new cultivars have been developed that generate more biomass than sorghum or wheat (Hiremath *et al.*, 2013). Studies in maize conducted by Li *et al.* (2018) and Ibraheem and El-Ghareeb (2019) reported that maize F1 hybrid showed strong heterosis for agronomic traits and increased biomass as compared to parents. These results are consistent with the ones reported by Singh *et al.* (2015) who indicated that cross-fertilization of parental lines with different genetic compositions results in hybrid vigor, which produces superior phenotypes with higher yield, accelerated growth rate and development, improved biomass, better quality, and improved resistance to biotic and abiotic stress. This also explains the high variability in biomass variables in maize compared to other cereals. With landraces, OPV, and commercial cultivars grown around the world, wide variation in biomass production is expected in maize.

Wheat accumulated less amounts of biomass and C compared to maize and sorghum for all the biomass and C variables, and this may be due to the low stature of the plant (Figure 3.1a). The crop size of wheat is generally smaller than that of maize and sorghum. In addition, Theocharis *et al.* (2012) reported that one of the main environmental stressors that restricts wheat growth and photosynthetic output and lowers grain yield is low temperature. Wheat is mainly grown in temperate regions and cold stress often extends the period of crop growth and lowers net photosynthetic rate and biomass accumulation (Whaley *et al.*, 2004; Yamori *et al.*, 2014; Li et at., 2015). Interestingly, wheat had higher root-to-shoot biomass ratios (Rb/Sb). However, the size of the wheat root systems remains lower than that for maize and sorghum, and as such the latter two crops will contribute more to carbon sequestration than wheat.

Sorghum has a comparable morphological structure and size to maize; however, its biomass production was consistently lower than that of maize. This may be due to the limited breeding of sorghum and the use of landraces that have not been targeted for genetic improvement (Hao *et al.*, 2021) when compared to maize which has received more investment. Therefore, sorghum may possess great untapped potential in breeding for biomass production. Investments in breeding sorghum for ethanol production with a limited focus on grain production have led to substantial genetic gains being achieved in biomass production of sorghum (Pfeiffer *et al.*, 2019). However, this has been limited to sweet sorghums for the industry, and the adoption of such varieties will not be beneficial to resource-poor farmers in drier areas where they depend on sorghum grain for food.

3.4.2 *Causes of variation in C accumulation and allocation amongst crop type*

Sorghum had higher total plant carbon stocks and carbon content than both maize and wheat which would make it a more efficient crop in increasing carbon fluxes from the atmosphere to the soil (Figure 3.1c and Figure 3.1d). Its big and fibrous root system will ensure deeper deposition of C in the soil which will be crucial for the long-term stability of SOC (Zuazo and

Pleguezuelo, 2009). The large and deep root system of sorghum of sorghum distinguishes its root architecture. According to Xiong *et al.* (2020), sorghum roots can reach soil depths of up to 2 m, whereas maize and wheat roots normally reach 1 m or less. Sorghum can reach and deposit organic matter, including carbon, in deeper soil horizons due to its more extensive and deeper root system. Because of its notable drought tolerance, sorghum develops deep roots as an adaptation strategy. Wheat and maize, on the other hand, have shallower root systems despite being sensitive to drought stress. Drought-stressed conditions can promote deeper root growth in sorghum, as Chadalavada *et al.* (2021) reported that when they observed sorghum roots extending deeper during dry spells. Sorghum's C4 photosynthetic pathway has higher photosynthetic efficiency and higher biomass production than wheat and maize's C3 photosynthetic pathways. In a study conducted by Xiao *et al.* (2021), they reported that sorghum produced 20% more aboveground biomass, resulting in enhanced carbon inputs into the soil profile.,

3.4.3 *Variations of plant biomass and carbon variables between crop type cultivars*

The variation between cultivars in root and shoot biomass could result from different specific allocation patterns caused by genetic variation between major cereal species. These patterns could be high shoot biomass production in maize, deep root systems, and balanced allocation of shoot and root biomass in sorghum and tillering in wheat (Irving, 2015). Maize had higher variability in Pb, Sb, and Rb between cultivars compared to sorghum and wheat (Figure 3.1a). Temperature, rainfall, nutrient availability, and soil type are all environmental factors that can have a substantial impact on carbon and biomass accumulation (Lin *et al.*, 2010, Mathew *et al.*, 2017). These environmental factors may cause maize cultivars to respond differently, resulting in variations in growth and allocation patterns. In a study conducted by Pittelkow *et al.* (2015) it was reported that the increase in biomass production from subtropical to tropical regions corresponds to increases in temperature and precipitation. These results are consistent with the ones reported in the current study as variability in Rb had a strong highest positive correlation with MAP and MAT (Table 3.8). Hence, lower precipitation limits root biomass production in temperate and subtropical climates, whereas low temperatures further limit biomass production in temperate climates.

Sorghum also exhibited high variability in Pb, Sb, and Rb between cultivars compared to wheat. This is due to sorghum's genetic diversity, there is a wide range of stem biochemical compositions suitable for different end purposes, such as bioenergy or fodder (Perrier *et al.*, 2017). Due to its resistance to drought, sorghum can sustain biomass production under water-stressed conditions. The wide differences in shoot biomass compared to root biomass for maize, sorghum, and wheat are due to their adaptations. Performance variations between genotypes represent genetic diversity, which is a result of the genotypes' diverse genetic backgrounds (Hughes *et al.*, 2008).

There was an increase in variation between cultivars of sorghum for Pcs (Figure 3.1c). Cultivars may respond differently to different treatments (Anderson-Teixeira *et al.*, 2013). This is proven by the decrease in variation between cultivars of maize for total Pcs by the different treatments like tillage, fertilizers, and environmental conditions that were applied across the studies. Wheat remains to be the crop with the lowest Pcs, Scs, and Rcs. There was no variation between genotypes for carbon content of all the crops, as all the varieties were constant (Figure 3.1b). Biomass and C allocation variability varied between roots and shoots as R/S ratios varied significantly amongst the wheat cultivars across the studies (Figure 3.1d). In a study conducted by Toscano *et al.* (2019) it was reported that heat-tolerant wheat genotypes exhibit a high R/S which indicates their capacity to sustain productivity even under conditions of simultaneous drought and heat stress. This allowed the heat-tolerant genotypes to allocate more biomass to root development than the heat susceptible genotypes. Such genotypes with high biomass accumulation and heat endurance are more appropriate for sub-Saharan Africa, where heat stress and drought are frequently co-occurring conditions.

3.4.4 *The links between variations of plant biomass and carbon variables*

The strong correlations of variability in Scs and Rcs and variability in Rb with PC1 shows that the three traits were the most important in explaining variation among the cereal varieties. Therefore, identifying shoot and root carbon stocks in varieties could be important in cultivar selection for carbon sequestration. Carbon content may be less effective in differentiating varieties as the carbon content in varieties is relatively constant and varies slightly between varieties and in most cases even crop types (Ma *et al.*, 2018). Maize varieties were correlated to the PC1 which showed that maize varieties exhibited most of the variation in this panel of cultivars while wheat varieties had the least variation. Sorghum varieties generally showed little differences which may be due to wide adaptation and stability in biomass production due to the wider genetic base that is observed in sorghum landraces. This presents sorghum as the crop with the greatest potential to be improved for biomass production which can be harnessed in new sorghum cultivars developed through hybrid breeding and new genomic technologies that will accelerate sorghum improvement (Hao *et al.*, 2021). There is high biomass production and carbon accumulation between maize cultivars but a low variableness in carbon enrichment in plant tissues. In contrast, wheat showed a high variableness in carbon enrichment but a low variableness in biomass production and C accumulation. Finally, Sorghum varieties did only marginally vary for plant C content and exhibited low variability in biomass and C accumulation.

The root-to-shoot ratios for biomass and carbon stocks showed a negative correlation. which indicates that the cultivars' variableness in the proportion of biomass and carbon allocated by cultivars to roots increases as the intensity of tillage increases, i.e. variableness is higher under tilled soils as compared to no-till ones, as well as under high-temperature areas.

3.5 Conclusion

The cultivars of maize and wheat showed significant intra-specific variation in biomass, carbon accumulation, and allocation to roots and shoots, demonstrating the importance of these genetic resources for the development of varieties with improved C sequestering potential. However, wheat presents the greatest potential for breeding to increase biomass production due to limited breeding in the crop. Using wheat as a model crop for increasing carbon sequestration can go a long way in mitigating the effects of climate change. Maize and sorghum will also remain important crops that can be used to support climate-smart agriculture. These findings improve our understanding of how C is allocated within plant tissues and possibly to soils, and they may be used as selection criteria for breeding crop varieties with high C sequestration capacity

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3.6 References

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CHAPTER 4: Water use efficiency of existing sorghum lines and wheat populations from sub-Saharan Africa

Abstract

Sorghum (*Sorghum bicolor* L. Moench) and wheat (*Triticun aestivum* L.) are among the most important crops grown in sub-Saharan Africa (SSA). With drought stress as one of the most pressing issues that results in low yield production, enhancing sorghum and wheat water-use efficiency (WUE) will improve food security in SSA. The main objective of this study was to evaluate the water use efficiency of sorghum and wheat for grain yield and for biomass production (both shoots and roots), with the ultimate goal of selecting drought tolerant genotypes for breeding. Fifty sorghum genotypes and 100 wheat genotypes were evaluated in the field using an alpha lattice design with three and two replications per genotype, respectively. The genotypes were compared on the basis of grain yield (GY), shoot biomass (SB), root biomass (RB), total plant biomass (PB) and for their respective water use efficiency: WUEGY, WUESB, WUERB, and WUEPB. Sorghum genotypes showed great differences in biomass production ranging from 0.56 to 164.13 g plant^{-1}, GY ranging from 0.59 to 12.88 g plant^{-1}, and WUE ranging from 0.63 to 0.001 g plant^{-1} mm^{-1}. Genotype AS115 produced the highest GY (12.88 g plant^{-1}) compared to all other evaluated genotypes. Genotype SS27 had the highest SB (137.83 g plant^{-1}), RB (137.83 g plant^{-1}) and PB, (164.13 g plant^{-1}) as well as the highest WUE. Grain yield exhibited positive significant correlation with HI and WUEGY ($p \leq 0.01$) for both wheat and sorghum. Among the fifty sorghum genotypes tested in this study, AS115, AS134, and AS251 had the highest grain yield production while using water efficiently while for wheat the top families were LM71 x BW152, LM75 x BW141 and LM70 x LM47. These genotypes should be used to generate new breeding populations to develop water use efficient cultivars for both sorghum and wheat.

Keywords: Biomass production; C sequestration; cereals; drought; grain yield; variability

4.1 Introduction

Sorghum (*Sorghum bicolor L.*) is the fifth most major cereal crop in the world and a staple food for more than 500 million people in more than 30 countries (Ahmed *et al.*, 2016). Sorghum serves as the primary food source for approximately 6% of people in Asia and Africa (Ranum *et al.*, 2014). In addition, 70-80% of animals that provide milk and meat for humans are fed with fodder and stover (Etuk *et al.*, 2012). Sorghum is grown on around 42.7 million acres of land, producing 58.7 million tonnes (Alikhani *et al.*, 2012). Approximately 33% of the sorghum grain produced worldwide is utilized for feeding livestock. Sorghum can grow and produce yield in regions with little rainfall and can withstand drought and heat stress better than other cereals such as maize and rice (Kenga *et al.*, 2006). The wide and deep roots system of sorghum, which can absorb water and nutrients to a depth of 3 m, are responsible for the plant's ability to withstand drought (Moroke, 2002; Moroke *et al.*, 2011).

Wheat is an important grain crop contributing 40% of the calorie intake and supporting 35% of the food intake of the global population (Upadhyay 2020; Grote *et al.*, 2021). Wheat production in sub-Saharan Africa (SSA) is vulnerable to drought impacts due to a heavy reliance on rain-fed agriculture and a lack of institutional capacity and water management strategies to respond to drought shocks (Lipper *et al.*, 2014; Tadesse *et al.*, 2018; Fava and Vrieling, 2021). Wheat experiences the greatest yield losses compared to the other major cereals including sorghum in terms of area affected by drought (Kim *et al.*, 2019). With wheat yield growth rates (1.5-1.7% per year) lagging behind, yield increase is required to meet global demand by year 2050 (Iizumi *et al.*, 2018), therefore interventions to increase resilience need to be promoted to reduce the impact of drought stress especially in resource poor regions such as SSA.

Drought is one of the most significant environmental elements affecting plant growth, development and productivity (Moosavi *et al.*, 2011; Mohammadai *et al.*, 2012). Drought reduces nutrient uptake by roots and induce nutrient deficiency by decreasing the diffusion rate of nutrients from soil to root, creating restricted transpiration rates and impairing of active transport and membrane permeability (Rouphael *et al.*, 2012). Although the effects of water stress on grain yield, plant growth, and development have been extensively investigated, little is known about how it may affect the physiological characteristics of seeds. It is critically essential to improve the water-use efficiency (WUE) of economically important crops, both for irrigated and rain-fed production (Hamdy *et al.*, 2003). Plant WUE can be defined broadly as the ratio of grain or biomass produced to total water used by the crop. To increase WUE in irrigated and rain-fed agriculture, several measures including mulching to reduce evaporation, drainage and lateral flow will need to be practiced. Others include better management of the water resource, changes in crop management and breeding for improved crop cultivars (Condon *et al.*, 2004; Wand *et al.*, 2002).

Breeding of crop varieties with high WUE presents a sustainable approach to increasing the resilience of sorghum and wheat production systems without major managerial changes from the farmers. Intraspecific variation in sorghum and wheat WUE has been observed and genetic variability can be assessed to identify superior genotypes with high WUE (Xin *et al.*, 2009). However, due to the complexity of these features and the absence of rapid and simple screening criteria and measuring procedures, robust measurement of WUE in field studies is difficult (Sinclair and Muchow, 1999). Limited studies have assessed how different sorghum and wheat varieties use water efficiently with most studies only focusing on water use efficiency by different cereals crops (Conley *et al.*, 2001; Sinclair *et al.*, 2005; Moroke *et al.*, 2011;). Blum, (2005) reported that increasing WUE by producing more biomass with the same amount of water is possible. These results align with Xin *et al.* (2009), who reported that WUE can be improved through improving biomass production. They also concluded that one effective method for selecting for high WUE in sorghum and wheat is to identify high-WUE genotypes based on biomass accumulation. Therefore, the objective of this study was to evaluate the water use efficiency of grain yield and for biomass production (both shoots and roots) of sorghum and wheat to select drought tolerant genotypes for breeding.

4.2 Methods and Materials

4.2.1 *Seedling establishment*

Sorghum

Fifty sorghum genotypes consisting of landraces, pure lines and a commercial hybrid were used in this study. Seeds of the 50 genotypes were planted in seedling trays filled with composited pinebark to a depth of 1 cm and raised in the greenhouse at the Controlled Environment Facility (CEF) at the University of KwaZulu-Natal in Pietermaritzburg, South Africa. The temperature inside the greenhouse was maintained at 25°C during the day and 15°C at night. Each genotype was planted in a single tray with three seeds planted per hole and later thinned to one seedling per plant. The seedlings were raised for three weeks before being transplanted to the field.

4.2.2 *Field trial establishment*

Sorghum

The field was ploughed and rotavated to ensure a fine tilth and efficient weed control. The test genotypes were transplanted into the field at the ARC Agricultural Engineering facility in Pretoria South Africa (Lat 25° 44' S and Long 28° 14' E). The trial was laid out in a 5 × 10 alpha lattice design with three replications. Each genotype was planted on a 2 m long plot spaced 90 cm apart, and plants were spaced 25 cm within the row. A single seedling was planted per individual planting station. Around the perimeter of the trial, border rows were established with the same spacing to reduce the risk of yield inflation in test plots in the outer rows. No additional water or fertilizer was applied after transplanting and the crop was rainfed from transplanting to maturity. The weather data for the growing period are recorded in Table 4.1.

Table 4 1: Monthly rainfall, maximum, minimum temperature, and relative humidity during 2022 growing seasons for the ARC-AE (Pretoria) research site from a nearby weather station

Month	Rainfall (mm)	Tmax (°C)	Tmin (°C)	Relative humidity (%)
Feb	33.53	29	17	62
Mar	18.54	27	16	62
Apr	173.48	25	12	61
May	16	23	8	56
Jun	16	20	5	54
Jul	0.76	20	4	53
Aug	2.2	23	7	46

Tmax = maximum temperature, Tmin = minimum temperature

Wheat

The field experiment was conducted at the University of KwaZulu-Natal Ukulinga Research Farm, located at 30°24'S, 29°24', 800 m above sea level using an alpha lattice design with two replicates per water regime (drought and non-drought stress). The average rainfall, temperature, and soil properties during the growing period were recorded. The soil bulk density was 1.04. The experiment was comprised of one plant population for each genotype × two watering regimes. Before planting the field was prepared to ensure fine tilth and weed control. The soil was covered with black plastic mulch to avoid rainwater infiltration into the soil profile. Irrigation was applied through a drip irrigation system with the aim to maintain soil water content at field capacity. The watermark sensors were used to determine the field capacity of the soil.

4.2.3 Data collection

Sorghum and wheat

Data was collected for biomass variables and grain yield. Shoot biomass (SB) was recorded as the total above-ground biomass cut from the base of the plant, excluding the grain. The shoots were oven-dried at 70°C for 48 hours, weighed and expressed in g m^{-2}. Root biomass (RB) was recorded as the total root dry matter harvested per genotype per plot. Root samples for each plot were harvested to a depth of 50 cm. Large roots were separated from the soil by hand and washed under running water to remove all soil particles. The remaining soil was mixed with water and the suspension was sieved through a 2 mm sieve. Fine roots were collected from the sieve residue and added to the large roots. The roots were oven-dried at 60°C for 72 hours. The dried roots were weighed on a balance to get the RB which was adjusted to g $plant^{-1}$. Total plant biomass (PB) was the sum of all dry plant material for each genotype including RB, SB and GY harvested from the test plots and recorded in g $plant^{-1}$. Root to shoot ratio (RS) was the ratio of the root biomass to the shoot biomass as recorded above. Grain yield (GY) was the weight of harvested grain at 12.5% moisture content per genotype per plot and expressed in g $plant^{-1}$. Harvest index (HI) was also calculated using the following formula:

$$HI = \frac{GY}{SB}$$

4.2.4 Water use efficiency computation

Water use efficiency was calculated using the amount of rainfall received by the plant during the growing season from planting to harvesting. Therefore, the water use efficiency for the different variables were calculated as shown below:

Grain yield water use efficiency (WUE_{GY}) = $\frac{\text{grain yield (g)}}{\text{amount of water applied(mm)}}$

Shoot biomass water use efficiency WUE_{SB} = $\frac{\text{shoot biomass (g)}}{\text{amount of water applied(mm)}}$

Root biomass water use efficiency (WUE_{RB}) = $\frac{\text{root biomass (g)}}{\text{amount of water applied(mm)}}$

Total plant biomass water use efficiency (WUE_{PB}) = $\frac{\text{total plant biomass (g)}}{\text{amount of water applied(mm)}}$

4.2.5 Data analysis

Summary statistics for sorghum and wheat parameters were generated using Genstat 20th edition. Correlation analyses, based on Pearson's correlations were carried out using IBM SPSS statistics to determine the strength of associations between variables.

4.3 Results

4.3.1 *Agronomic performances based on biomass allocation and water use efficiency*

The agronomic performance for the top 10 and bottom five sorghum and wheat genotypes are shown on Table 4.2 and Table 4.3, respectively. The sorghum genotype that used water more efficiently for grain yield production was AS115 with the maximum value of WUE_{GY} of 0.0494 g plant^{-1} mm^{-1}, with the highest grain yield and HI of 12.88 g plant^{-1} and 60.23%, respectively. The second and third genotypes that used water more efficiently for grain yield production were genotype AS134 and AS251 with values of 0.0472 and 0.0409 g plant^{-1} mm^{-1}, respectively. On the other hand, for wheat families LM71 x BW152, LM75 x BW141 and LM70 x LM47 were the most water efficient in producing grain. Family LM71 x BW152 was also the most efficient genotype in generating RB. For sorghum, genotype SS27 was the seventh genotype that had a highest WUEgy compared to all the genotypes, but had the highest values PB, SB, and RB compared to all the ten genotypes with the values of 164.13, 137.83, and 26.29 g plant^{-1}, respectively, with the lowest HI of 6.05%. Genotype SS27 also had the highest WUEPB, WUESB, WUERB compared to all the ten genotypes with the values of 0.6300, 0.5291, and 0.1009 g plant^{-1} mm^{-1}, respectively. But for wheat, family BW141 x LM71 was the most efficient in producing SB and PB. Genotype AS251 was amongst the best performing genotypes for WUEGY but had the lowest SB and highest RB/SB compared to all the ten genotypes with values of 19.50 and 0.52 g plant^{-1}, respectively. Genotype AS136 was the tenth best performing genotype for WUEGY with the value of 0.0288 g plant^{-1} mm^{-1}, but had the lowest grain yield and biomass accumulated to the roots compared to all the ten genotypes with values of 7.50 and 3.06 g plant^{-1}, respectively. Genotype AS130 had the lowest RB/SB compared to all the ten genotypes with the value of 0.10 and was the fifth best performing genotype for WUEGY with the value of 0.0338 g plant^{-1} mm^{-1}.

Table 4.2: Agronomic performances and water use efficiency of the top and bottom sorghum genotypes ranked according to water use efficiency for grain yield

Genotype	PB	SB	RB	RB/SB	GY	HI	WUEPB	WUESB	WUERB	WUEGY
Top 10 experimental genotypes										
AS115	25.38	21.38	4	0.19	12.88	60.23	0.0974	0.0821	0.0154	0.0494
AS134	43.36	39.07	4.29	0.11	12.29	31.44	0.1664	0.15	0.0165	0.0472
AS251	29.67	19.5	10.17	0.52	10.67	54.7	0.1139	0.0749	0.039	0.0409
AS132	29.61	22	7.61	0.35	10.56	47.98	0.1137	0.0844	0.0292	0.0405
AS130	39.16	35.52	3.64	0.1	8.81	24.8	0.1503	0.1363	0.014	0.0338
AS138	48.93	35.36	13.56	0.38	8.54	24.14	0.1878	0.1357	0.0521	0.0328
SS27	164.13	137.83	26.29	0.19	8.33	6.05	0.63	0.5291	0.1009	0.032
AS203	43.52	31.83	11.69	0.37	8.29	26.03	0.1671	0.1222	0.0449	0.0318
AS145	32.33	26.58	5.75	0.22	8.21	30.88	0.1241	0.102	0.0221	0.0315
AS136	31.5	28.44	3.06	0.11	7.5	26.37	0.1209	0.1092	0.0118	0.0288
Bottom 5 experimental genotypes										
AS116	20.15	14.45	5.7	0.39	1.15	7.96	0.0773	0.0555	0.0219	0.0044
AS563	38.81	35.5	3.31	0.09	1.06	2.99	0.149	0.1363	0.0127	0.0041
NW5393	61.99	54.89	7.11	0.13	0.84	1.52	0.238	0.2107	0.0273	0.0032
ICSV92001	41.79	37.8	3.99	0.11	0.64	1.69	0.1604	0.1451	0.0153	0.0024
AS143	14.69	12.1	2.59	0.21	0.59	4.84	0.0564	0.0464	0.01	0.0022

PB = plant biomass, SB = shoot biomass, RB = root biomass, RB/SB = root to shoot ratio, GY = grain yield, HI = harvest index, WUE_{PB} = water use efficiency for plant biomass, WUE_{SB} = water use efficiency for shoot biomass, WUE_{RB} = water use efficiency for root biomass, WUE_{GY} = water use efficiency for grain yield.

Table 4.3: Agronomic performances and water use efficiency of the top and bottom wheat genotypes ranked according to water use efficiency for grain yield

Genotype	PB	SB	RB	RB/SB	GY	HI	WUE$_{PB}$	WUE$_{SB}$	WUE$_{RB}$	WUE$_{GY}$
	top 10 experimental genotypes									
LM71 x BW152	30.00	26.00	4.00	0.15	26.00	41.94	0.38	0.33	0.05	0.33
LM75 x BW141	27.00	26.00	1.00	0.04	24.00	35.29	0.34	0.33	0.01	0.31
LM70 x LM47	19.33	16.67	2.67	0.16	20.67	44.93	0.25	0.22	0.03	0.26
BW141 x LM71	47.00	46.00	1.00	0.02	20.00	23.81	0.60	0.59	0.01	0.25
BW162 x BW140	14.50	14.00	0.50	0.04	19.00	50.00	0.18	0.17	0.01	0.24
BW162 x BW152	11.00	10.00	1.00	0.10	18.00	50.00	0.14	0.13	0.01	0.23
BW152 x LM71	17.00	14.00	3.00	0.21	16.00	37.21	0.22	0.18	0.04	0.20
LM26 x BW141	23.00	22.00	1.00	0.05	14.00	30.43	0.29	0.28	0.01	0.18
LM26	15.50	15.00	0.50	0.03	14.00	41.18	0.20	0.19	0.01	0.18
LM71 x BW140	14.00	12.00	2.00	0.17	13.33	44.44	0.18	0.15	0.03	0.17
	bottom 5 experimental genotypes									
BW141 x LM75	8.40	7.20	1.20	0.17	0.40	5.00	0.11	0.09	0.02	0.01
LM75 x BW162	8.00	6.40	1.60	0.25	0.40	5.88	0.10	0.08	0.02	0.01
BW152 x BW140	9.20	7.20	2.00	0.28	0.40	4.76	0.12	0.09	0.03	0.01
BW141 x BW162	8.40	8.00	0.40	0.05	0.20	2.17	0.11	0.10	0.01	0.00
LM48 x LM47	9.60	8.00	1.60	0.20	0.20	2.38	0.12	0.11	0.02	0.00

PB = plant biomass, SB = shoot biomass, RB = root biomass, RB/SB = root to shoot ratio, GY = grain yield, HI = harvest index, WUE$_{PB}$ = water use efficiency for plant biomass, WUE$_{SB}$ = water use efficiency for shoot biomass, WUE$_{RB}$ = water use efficiency for root biomass, WUE$_{GY}$ = water use efficiency for grain yield.

The bottom five genotypes that used water less efficiently for grain yield production were AS116, AS563, NW5393, ICSV92001, and AS143, with genotype AS143 having the lowest WUEGY compared to all the genotypes with the value of 0.0022 g plant^{-1} mm^{-1}. Genotype AS143 also had the lowest PB, SB, RB, and GY compared to all the genotypes with the quantities of 14.69, 12.10, 2.59, and 0.59 g plant^{-1}, respectively. Genotype AS143 also had the lowest WUEPB, WUESB, and WUERB compared to all the genotypes with the values of 0.0564, 0.0464, and 0.0100 g plant^{-1} mm^{-1}, respectively.

4.3.2 Plant parameters and water use efficiency for sorghum and wheat lines

The summary statistics of sorghum and wheat plant parameters and water use efficiency for different sorghum genotypes are summarized in Table 4.4 and Table 4.5. Plant biomass (PB) for sorghum ranged from 14.69 g of dry matter per plant (g plant^{-1}) to 164.13 g plant^{-1} whereas for wheat it was lower and ranged from 0.33 g plant^{-1} to 47.00 g plant^{-1}. The PB mean value for sorghum was 38,24 g plant^{-1} and the median was 31,38 g plant^{-1} while for wheat it was 10.26 g plant^{-1} and 9.60 g plant^{-1} respectively. The coefficient of variation for SB was 4 times greater than the one for PB, with the amount of 65.61% for sorghum while that for wheat was comparable. Shoot biomass portrayed positive skewness for both wheat and sorghum. Root biomass (RB) was higher for sorghum (0.90 g plant^{-1}) than wheat (0.02 g plant^{-1}). However, the trend was reversed for grain yield with wheat (4.90 g plant^{-1}) having a higher mean than sorghum (4.79 g plant^{-1}).

Table 4.4: Summary statistics on sorghum plant parameters, and water use efficiency of sorghum

Statistics	Plant parameters									
	PB	SB	RB	RB/SB	GY	HI	WUE_{PB}	WUE_{SB}	WUE_{RB}	WUE_{GY}
Mean	38.24	32.35	5.9	0.2	4.79	17.95	0.15	0.12	0.02	0.02
Median	31.38	26.56	4.45	0.19	4	14.8	0.12	0.1	0.02	0.02
Min.	14.69	12.1	0.56	0.02	0.59	1.52	0.05	0.05	0	0
Max.	164.13	137.83	26.29	0.52	12.88	60.23	0.63	0.53	0.1	0.05
Q1	25.38	21.09	3.32	0.11	2.84	7.68	0.1	0.08	0.01	0.01
Q3	42.96	35.47	7.33	0.23	6.36	24.62	0.16	0.14	0.03	0.02
st dev	24.11	21.22	4.25	0.11	3.05	13.26	0.09	0.08	0.02	0.01
Var	581.16	450.49	18.08	0.01	9.31	175.88	0.01	0.01	0	0
CV (%)	63.04	65.61	72.13	54.96	63.7	73.9	63.96	65.61	72.13	64.67
Skewness	3.34	3.17	2.51	0.83	0.85	1.41	3.26	3.17	2.51	0.89
kurtoisis	14.62	12.67	9.38	0.21	0.26	2.11	14.21	12.67	9.38	0.28

Min = minimum, Max = maximum, Q1 and Q3 = first and third quartile, st dev = standard deviation, Var = variance, CV = coefficient of variation, PB = plant biomass (g plant^{-1}), SB = shoot biomass (g plant^{-1}), RB = root biomass (g plant^{-1}), RB/SB = root to shoot ratio, GY = grain yield (g plant^{-1}), HI = harvest index, WUE_{PB} = water use efficiency for plant biomass (g plant^{-1}mm^{-1}), WUE_{SB} = water use efficiency for shoot biomass(g plant^{-1}mm^{-1}), WUE_{RB} = water use efficiency for root biomass(g plant^{-1}mm^{-1}), WUE_{GY} = water use efficiency for grain yield(g plant^{-1}mm^{-1}).

Table 4.5: Summary statistics on plant parameters, and water use efficiency of wheat

Statistics	Plant parameters									
	Pb	Sb	Rb	Rb/Sb	Gy	HI	WUE_{PB}	WUE_{SB}	WUE_{RB}	WUE_{GY}
Mean	10.26	9.00	1.63	0.20	4.90	25.92	0.13	0.12	0.02	0.06
Median	9.60	8.13	1.50	0.17	4.00	25.93	0.12	0.10	0.02	0.05
Min.	0.33	0.50	0.17	0.02	0.20	1.85	0.00	0.01	0.00	0.00
Max.	47.00	46.00	6.00	1.33	26.00	59.52	0.60	0.59	0.08	0.33
Q1	7.43	6.40	0.80	0.11	2.40	17.65	0.09	0.08	0.01	0.03
Q3	12.00	10.00	2.00	0.25	6.00	33.33	0.15	0.13	0.03	0.08
Stdev	5.16	4.61	1.08	0.14	3.80	11.17	0.07	0.06	0.01	0.05
Var	26.67	21.23	1.16	0.02	14.41	124.90	0.00	0.00	0.00	0.00
CV	50.24	51.10	66.06	72.67	77.41	43.05	50.30	51.18	66.06	77.41
Skewness	2.91	4.05	1.31	2.76	2.02	0.03	2.90	4.04	1.31	2.02
Kurtosis	17.18	26.84	2.06	14.35	5.83	-0.40	17.13	26.78	2.06	5.83

Min = minimum, Max = maximum, Q1 and Q3 = first and third quartile, st dev = standard deviation, Var = variance, CV = coefficient of variation, PB = plant biomass (g plant^{-1}), SB = shoot biomass (g plant^{-1}), RB = root biomass (g plant^{-1}), RB/SB = root to shoot ratio, GY = grain yield (g plant^{-1}), HI = harvest index, WUE_{PB} = water use efficiency for plant biomass (g plant^{-1}mm^{-1}), WUE_{SB} = water use efficiency for shoot biomass(g plant^{-1}mm^{-1}), WUE_{RB} = water use efficiency for root biomass(g plant^{-1}mm^{-1}), WUE_{GY} = water use efficiency for grain yield(g plant^{-1}mm^{-1}).

The maximum value for water use efficiency for shoot biomass (WUESB) was 0.53 g plant^{-1} mm^{-1} and the minimum value was 0.05 g plant^{-1} mm^{-1}. The mean for WUESB was 0.12 g plant^{-1} mm^{-1}, which was 17% lower than that of WUEPB. There was also very small variation between genotypes for WUESB compared to WUEPB, with standard deviation and variance of 0.08 and 0.01, respectively. The minimum value of WUERB was 0.002 g plant^{-1} mm^{-1}. The maximum value of WUERB was 0.101 g plant^{-1} mm^{-1}. There is little variation between genotypes for WUERB, with the standard deviation and variance of 0.016 and 0.0003, respectively, and these values are very small in comparison to those of WUESB in both wheat and sorghum. The skewness value of WUERB was lower than that of WUESB, with the positive skewness value of 2.51. The maximum value of WUEGY was 0.049 g plant^{-1} mm^{-1} and the minimum value was 0.002 g plant^{-1} mm^{-1}. The mean for WUEGY was 0.018 g plant^{-1} mm^{-1}, which was 13% lower than that of WUEPB. The first and third quartiles of WUEGY were at the lower values compared to WUEPB, which were at values of 0.010 and 0.024 g plant^{-1} mm^{-1}, respectively. There is also almost no variation between genotypes for WUEGY, with the standard deviation and variance of 0.01180 and 0.0001, respectively, and these values are very much small in comparison to those of WUEPB.

4.3.3 Associations between plant parameters and water use efficiency

Plant biomass exhibited a significant positive correlation with WUEPB, WUESB, and WUERB (rs = 1.00, 0.96, and 0.53; respectively; $p \leq 0.01$) (Table 4.6 and Table 4.7), proving a direct link between the WUE variables (Table 4.4). Plant biomass also showed a non-significant correlation with WUEGY. All plant variables showed positive association with all the WUE variables (WUEPB, WUESB, and WUERB), while they had a positive non-significant correlation with WUEGY. Shoot biomass was strongly associated with WUESB compared to WUEPB, and RB was strongly associated with WUEPB compared to WUESB. Grain yield exhibited positive non-significant correlation with WUEPB and WUESB in contrast to HI, which exhibited negative significant correlation with WUEPB and WUESB. GY and HI also exhibited significant correlation with WUEGY (rs = 1.00 and 0.80; respectively; $p \leq 0.01$).

Table 4.6: Spearman rank correlation displaying relationship between plant parameters and water use efficiency of sorghum

Traits	**PB**	**SB**	**RB**	**RB/SB**	**GY**	**HI**	**WUE_{PB}**	**WUE_{SB}**	**WUE_{RB}**	**WUE_{GY}**
Pb	1									
SB	0.96**	1								
RB	0.53**	0.32*	1							
RB/SB	-0.20	-0.44**	0.68**	1						
GY	0.21	0.18	0.19		1					
HI	-0.30*	-0.34*	0.01	0.24	0.79**	1				
WUE_{PB}	1.00**	0.95**	0.55**	-0.17	0.21	-0.30*	1			
WUE_{SB}	0.96**	1.00**	0.32*	-0.44**	0.18	-.34*	0.95**	1		
WUE_{RB}	0.53**	0.32*	1.00**	0.68**	0.19	0.01	0.55**	0.32*	1	
WUE_{GY}	0.20	0.16	0.19	0.02	1.00**	.80**	0.19	0.16	0.19	1

PB = plant biomass, SB = shoot biomass, RB = root biomass, RB/SB = root to shoot ratio, GY = grain yield, HI = harvest index, WUEPB = water use efficiency for plant biomass, WUE_{SB} = water use efficiency for shoot biomass, WUE_{RB} = water use efficiency for root biomass, WUE_{GY} = water use efficiency for grain yield. * and ** denote significant at 0.05 and 0.01, respectively

Table 4.7: Spearman rank correlation displaying relationship between plant parameters and water use efficiency of wheat

Traits	PB	RB	SB	RB/SB	GY	HI	WUE_{PB}	WUE_{RB}	WUE_{SB}	WUE_{GY}
PB	1									
RB	0.94**	1								
SB	0.52**	0.30**	1							
RB/SB	0.06	-0.21**	0.83**	1						
GY	0.23**	0.25**	0.07	-0.05	1					
HI	-0.17**	-0.20**	-0.10	0.02	0.85**	1				
WUE_{PB}	1.00**	0.94**	0.53**	0.07	0.23**	-0.17**	1			
WUE_{RB}	0.95**	1.00**	0.31**	-0.20**	0.25**	-0.19**	0.94**	1		
WUE_{SB}	0.53**	0.32**	0.97**	0.79**	0.05	-0.13*	0.53**	0.33**	1	
WUE_{GY}	0.22**	0.25**	0.07	-0.06	1.00**	0.84**	0.23**	0.25**	0.05	1

PB = plant biomass, SB = shoot biomass, RB = root biomass, RB/SB = root to shoot ratio, GY = grain yield, HI = harvest index, WUE_{PB} = water use efficiency for plant biomass, WUE_{SB} = water use efficiency for shoot biomass, WUE_{RB} = water use efficiency for root biomass, WUE_{GY} = water use efficiency for grain yield. * and ** denote significant at 0.05 and 0.01, respectively

4.4 Discussion

4.4.1 *Effects of genotypes on grain yield*

Genotype AS115 exhibited the highest grain yield compared to all the genotypes. This might be due to the fact that genotype AS115 might have been amongst the genotypes that was well watered. Well-watered plants tend to have the highest grain yield. Ahmed (2009) stated that this is due to susceptible water stress and seed weight. The high grain yield on genotype AS115 might be due to the higher number of grains per head, since genotype had a slightly high shoot biomass (21.38 g plant^{-1}) (Table 4.2). In a study conducted by George-Jaeggli *et al.* (2011), they reported that seed number is the most crucial yield component associated with increases in yields of sorghum. In this study, high grain yield was associated with the high shoot biomass; and this aligns with the study that was conducted by George-Jaeggli *et al.* (2011), where increased plant height was associated with increased grain yield via an effect on shoot biomass. According to van Oosterom and Hammer (2008), grain number of sorghum is closely correlated with panicle development rate and crop growth rate at anthesis. As a result, an earlier onset of drought stress in circumstances where pre-anthesis water use is higher could be detrimental to grain number. The most pressing issue for low grain yield is drought stress. A variety of various morphological and physiological features of a genotype, which are in turn impacted by water availability, all have an impact on grain yield. A crucial factor in the selection of high yielding genotypes is the harvest index (HI), which is the proportion of grain production to total above-ground plant biomass. A plant's ability to transform biological yield into economic yield is also indicated by a high HI (Kusalkar *et al.*, 2003). Genotype AS143 had the lowest grain yield of 0.59 g plant^{-1} (Table 4.2), this is due to low accumulation of biomass to roots and shoots. Genotype AS145 also had a HI of 4.84% (Table 4.2). Only a combination of a minimum biomass reduction and an increase in HI will prevent losses in grain production per plant (George-Jaeggli *et al.*, 2011). According to observations for maize (Zea mays L.), wheat, and soybean (Glycine max L.), grain yield formation is typically sink-limited rather than source-limited (Borras *et al.*, 2004). Although sorghum's potential yield and biomass production are frequently resource limited (Gambin and Borras, 2007), grain numbers are vulnerable to stress because of moisture limitation. There are studies that have also demonstrated a strong link between grain yield and grain numbers with just a minimal impact of stress on individual grain mass (Craufurd and Peacock, 1993; Heiniger *et al.*, 1997).

An important screening and breeding method is the use of phenotypic expression to exploit genetic variability. The environment heavily influences how phenotypic differences manifest, and this variability is exacerbated by the fact that genotypes respond to environmental changes differently because no two environments are exactly alike (Mutava *et al.*, 2011). The genotypes showed significant variation for biomass and grain yield production, this might be due to different factors like, some genotypes might have not received enough sunlight, water, and some might have been affected by weeds and pests. Differences in performance of various genotypes could be attributed to higher rainfall amounts and better distribution resulting in adequate moisture and favourable temperatures during panicle development and flowering (Table 4.1).

4.4 2 *Effects of genotypes on water use efficiency*

Table 4.2 shows the average water use efficiency as displayed by sorghum genotypes. An estimate of water use efficiency is given by the relationship between water utilized in evapotranspiration and dry matter production (Mastrorilli *et al.*, 1999). The genotypes that were more efficient in their water use for grain production were AS115, AS134, and AS251. This is due to the high values of grain yield that were produced by the three genotypes, and these results are consistent with the ones obtained by Naim *et al.* (2010), where they observed that the increased water use efficiency was due to increased seed yield of the crop. The genotypes that used water less efficiently for grain yield production were AS143 and ICSV9001. This is due to the low production of grain yield production by the genotypes. This might also be due to the fact that sorghum was grown during summer, which means they experienced a great degree of heat stress, resulting to an increased water demand. The amount of depletion below a threshold soil water content value that initiates stress, such as 50%, and its timing associated with growth stage sensitivity, evaporative requirement, root density, and soil texture are factors that determine how severe the yield reduction caused by water stress is (Howell, 2001). Some genotypes had a high-water use efficiency for plant biomass but then had a low water use efficiency for grain yield, this means that some genotypes used more water to only produce low grain yields. These results are in contrast with the ones reported by Conley *et al.* (2001), where they discovered that yield increase is likely without additional use of water resources at higher than present day ambient CO2 concentrations. These data suggest an increasing WUE trend due to CO2 enrichment exists with increasing drought. Genotypes that had high water use efficiency for shoot biomass tend to have a low water use efficiency for grain yield, but those with a low water use efficiency for root biomass also had a low WUE for grain yield. In a study conducted by Narayanan *et al.* (2013), they reported that there are variations in WUE amongst sorghum genotypes in the field and that higher WUE based on biomass production per unit water usage is associated to higher biomass production rather than lower water use. This is consistent with the current study since high accumulation of biomass in the roots and shoot lead to high WUE for plant, shoot, and root biomass. The findings of this study suggest that WUE could be increased while maintaining the capacity for biomass production and yield. The genotypes of sorghum used in this study provide valuable plant resources for figuring out what causes enhanced WUE. The increased plant biomass production (164.13 g plant^{-1}) on genotype SS27 (Table 4.2) may be due to the fact that sorghum is a tall plant with relatively high plant heights. These results are confirmed by the study conducted by George-Jaeggli *et al.* (2011) where they reported increased biomass production in tall sorghum genotypes. Tall sorghum genotypes that produce more biomass may have open canopies that are more productive and allow more light to reach the mid-canopy levels (Pattey *et al.*, 1991; Rochette *et al.*, 1996). Tall genotypes had higher biomass and WUE, which suggests that manipulating plant height could increase sorghum yield potential under rainfed conditions (Narayanan *et al.*, 2013).

4.4.3 *The correlations between plant parameters and WUE for sorghum*

A significant correlation for PB with WUEPB, WUESB, and WUERB was observed but not with WUEGY. This is in contrast with the results reported by Xin *et al.* (2009), who mentioned that WUEGY can be influenced by biomass production. There was a strong link for SB with WUESB, whereas there was a strong link for RB with WUEPB. Water use was not significantly correlated with water use efficiency but was strongly correlated with biomass. Generally, the rank of the lines in biomass production and WUE was consistent.

4.5 Conclusion

Overall, sorghum with high biomass production and WUE, such as, AS115, AS134, AS251, AS132, and AS130 genotypes, can be bred to produce bioenergy and forage. The top wheat families such as LM71 x BW152, LM75 x BW141 and LM70 x LM47 with the highest grain yield production while using water efficiently should be used to generate new breeding populations to develop water use efficient cultivars for both sorghum and wheat. Nevertheless, more research is required to increase grain based WUE by converting biomass production to increasing grain yield and enhancing harvest index. Future studies should also investigate the link of WUE with biomass and water use under various degrees of water stress. In conclusion, we found significant genetic variation in sorghum genotypes for biomass production and WUE in this study. The genotypes of sorghum and wheat used in this study to assess biomass, yield, and WUE provide essential plant materials for determining the mechanisms underlying variations in these traits.

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CHAPTER 5: Response of sorghum (*Sorghum bicolar* (L.) Moench) and maize (*Zea mays*) genotypes for agronomic traits and atmospheric carbon sequestration

Abstract

Crops store a significant amount of carbon (C) and thus can play a critical role for mitigating climate change. Crop roots are the primary C source in agricultural soils, and they are particularly vital for long-term C storage in agroecosystems. The objective of this study was to assess agronomic performances, plant biomass and carbon accumulation in root and shoot of sorghum and maize genotypes to select better performing breeding parents. Fifty and forty-five genotypes of sorghum and maize were evaluated at two different sites. Data was collected for total plant biomass (PB), shoot biomass (SB), root biomass (RB), root-to-shoot biomass ratio (R/S), grain yield (GY), harvest index (HI), total plant carbon stock (Pcs), shoot carbon stock (Scs), root carbon stock (Rcs), root-to-shoot carbon stock ratio (Rcs/Scs), grain carbon content (Gcc), shoot carbon content (Scc), and root carbon content (Rcc). There was a significant genetic variation in GY, HI, Gcs, Scc, Rcc, and Gcc ($P < 0.05$) for sorghum. There was a significant genetic variation in maize for all the agronomic traits and carbon variables ($P < 0.05$) except for RB, R/S, Rcc, and Gcc. Genotype AS115 produced the highest GY and Gcs (12.88 g plant^{-1} and 5.61 g plant^{-1}, respectively) compared to all the other genotypes, the trend is the same with maize genotype TZECOMP3DT/WHITEDTSTRSY-CZ (172.13 g plant^{-1} and 81.65 g plant^{-1}, respectively). Genotype SS27 had the highest SB (137.83 g plant^{-1}), RB (137.83 g plant^{-1}) and PB, (164.13 g plant^{-1}) and ranked first for all the carbon variables except Gcs, Rcc, and Gcc. Genotype AS251 had the highest R/S and Rcs/Scs (0.52 and 0.50, respectively) compared to all the assessed genotypes. Grain yield showed higher positive correlations with HI and Gcs ($r = 0.87$ and 1.00, respectively) in sorghum. Root biomass had a positive correlation with all the agronomic traits and carbon variables except for Rcc and Gcc in sorghum. The current study demonstrated that genotypes store more C into their shoots than their roots and selection of sorghum and maize genotypes based on biomass production and allocation will allow for a more effective selection of high yielding and carbon sequestration potential.

Keywords: Carbon sequestration; sorghum; maize, biomass production

5.1 Introduction

carbon (C) storage has become an increasingly relevant subject in agriculture due to its potential to mitigate climate change through the sequestration of atmospheric carbon dioxide (CO_2) into soils and plant biomass. Sorghum (*Sorghum bicolar (L.) Moench*) and maize (*Zea mays*) are two essential crops that have been found to have substantial capacity for carbon storage in agricultural systems (Xiang *et al.,* 2017). Agricultural soils could play an important role in this attempt since they cover up to 34% of the land surface (Ritchie and Roser, 2020) and management has a significant impact on soil organic C storage by changing inputs and decomposition rates (Janzen, 2015; Paustian *et al.,* 2016). Concerns over rising CO_2 levels in the atmosphere have sparked interest in carbon flow in terrestrial ecosystems, as well as the latter's capacity for higher soil carbon sequestration (Daba and Dejene, 2018). The high carbon losses in cultivated crop land are due to the removal of most plant residues after harvest and high decomposition rates due to insufficient nutrient supply to soils (Poeplau and Don, 2015). Approximately 17% of all atmospheric CO_2 flows through the plant-soil-atmosphere interaction each year making soil and plant C critical to the global C cycle (Bruggemann *et al.,* 2017). Root C is a major contributor to soil organic C, accounting for up to 90% of all C inputs to arable soils (Katterer *et al.,* 2011). Root C has a longer residence period in soil than C derived from above ground crop residue and manure (Katterer *et al.,* 2011; Menichetti *et al.,* 2015; Zhang *et al.,* 2015) due to its resistant chemical composition (Rasse *et al.,* 2005) and preferential absorption into more stable fractions (Ghafoor *et al.,* 2017). Because of the low decomposer abundance and high storage capacity of deep unsaturated layers (Rumpel *et al.,* 2012; Sanaullah *et al.,* 2016), root C inputs to deep soil have been related to long-term C storage (Russell *et al.,* 2009; Fan *et al.,* 2019). Therefore, promoting more and deeper roots has been advised as an approach to mitigate climate change, with an estimated potential to remove 1 Pg yr^{-1} of atmospheric CO_2 (Lynch and Wojciechowski, 2015; Paustian *et al.,* 2016; Pierret *et al.,* 2016). Thus, it is critical to understand how management might improve root C inputs to agricultural soils to not only sequester C over time, but also to drive C dynamics, thus increasing the numerous benefits of soil organic matter for agricultural soils (Janzen, 2015; Paustian *et al.,* 2016).

Plant C allocations vary significantly across plant species and crop varieties (Gonzalez-Sanchez *et al.,* 2012). The differences are important in the ultimate deposition of plant C into soil and can be exploited to choose crop types and varieties with increased C sequestration capability. The need to adjust agricultural practice to increase biomass production to sequester atmospheric CO_2 is a desirable goal. Several studies have assessed the potential of sorghum and maize genotypes for C storage. For example, according to Xiang *et al.* (2019) reported that growing sorghum varieties with high biomass can significantly increase carbon sequestration in soils. In another experiment conducted by Liang *et al.* (2020), it was revealed that maize varieties with high yield potential have a greater capacity to store C in biomass and soil.

Sorghum and maize are among South Africa's and world's most widely cultivated crops. Understanding how different genotypes of these crop species interact with the atmosphere in terms of C sequestration can have far-reaching consequences for sustainable land use and climate mitigation measures. By assessing variations in C sequestration potential among sorghum and maize genotypes, genotypes that are more effective at capturing and storing CO_2 from the atmosphere can be selected. This knowledge has ramifications for crop breeding and selection, as well as agronomic approaches that can improve carbon sequestration capability. Furthermore, such research can help to guide policy decisions and agricultural practices that are consistent with global efforts to reduce greenhouse gas emissions and achieve carbon neutrality. Hence, the objective of this study was to assess agronomic performances, plant biomass and carbon accumulation in root and shoot of sorghum and maize genotypes to select better performing breeding parents. This will facilitate selection of varieties with superior characteristics for C sequestration amid climate change and soil degradation challenges currently faced around the country. Plants are the conduit between the atmosphere and the soil and play an irreplaceable role of transferring carbon to the soil. The positive impact of long-term storage of C in the soil include reduced atmospheric carbon concentration, increased water and moisture retention capacity of the soil and improved soil structure for nutrient and water recycling.

5.2 Methods and materials

5.2.1 *Planting material and seedling establishments*

Fifty sorghum and forty-five maize genotypes consisting of landraces, pule lines and a commercial hybrid were used in this study. Seeds of the 50 sorghum genotypes were planted in seedling trays filled with composited pine bark to a depth of 1 cm and raised in the greenhouse at the Controlled Environment Facility (CEF) at the University of KwaZulu-Natal in Pietermaritzburg, South Africa. The temperature inside the greenhouse was maintained at 25ºC during the day and 15ºC at night. Each genotype was planted in a single tray with three seeds planted per hole and later thinned to one seedling per plant. The seedlings were raised for three weeks before being transplanted to the field.

5.2.2 *Field trial establishment*

Environment 1: Pretoria Field Experiment (Sorghum)

The field was ploughed and rotated to ensure a fine tilth and efficient weed control. The fifty sorghum genotypes were transplanted into the field at the ARC Agricultural Engineering facility in Pretoria, South Africa (Lat 25° 44' S and Long 28° 14' E). The mean annual temperature and mean annual precipitation for Pretoria are 18.4 ℃ and 661 mm, respectively. The trial was laid out in randomized complete block design with three replications. Each genotype was planted on a 2 m long plot spaced 90 cm apart, and plants were spaced 50 cm within the row. A single seedling was planted per individual planting station. Around the perimeter of the trial, border rows were established with the same spacing to reduce the risk of yield inflation in test plots in the outer rows. No additional water or fertilizer was applied after transplanting and the crop was rainfed from transplanting to maturity. The soil in Pretoria is classified as red apedal, with good drainage. The weather data for the growing period are recorded in Table 5.1.

Table 5.1: Pretoria monthly rainfall, maximum, minimum temperature, and relative humidity during 2022 growing seasons of sorghum for the research site from a nearby weather station.

	Rainfall	Tmax (°C)	Tmin (°C)	Relative humidity (%)
Feb	33.53	29	17	62
Mar	18.54	27	16	62
Apr	173.48	25	12	61
May	16	23	8	56
Jun	16	20	5	54
Jul	0.76	20	4	53
Aug	2.2	23	7	46

Environment 2: Ukulinga Field Experiment (Maize)

The University of KwaZulu-Natal's Ukulinga Research Farm and the Controlled Environment Facility at the Pietermaritzburg campus was used for the growing of maize genotypes. The long-term average temperature and rainfall for Ukulinga (LAT: 29.667° LON: 30.406° and ALT: 811 m) are 16.7 °C and 966 mm, respectively. The forty-five maize genotypes were also planted in a randomized complete block design with two replications. Each genotype was planted on a 2 m long plot spaced 90 cm apart, and plants were spaced 50 cm between rows. The soil at Ukulinga farm is loam, fertile and friable with good drainage and a pH of 4.5. However, it is susceptible to cracking and crusting under flooding.

5.2.3 Data collection

5.2.3.1 *Biomass and Grain yield data collection*

Data was collected for biomass variables and grain yield. Shoot biomass (SB) was recorded as the total above-ground biomass cut from the base of the plant, excluding the grain. The shoots were oven-dried at 70°C for 48 hours, weighed and expressed in g plant^{-1}. Root biomass (RB) was recorded as the total root dry matter harvested per genotype per plot. Root samples for each plot were harvested to a depth of 50 cm. Large roots were separated from the soil by hand and washed under running water to remove all soil particles. The remaining soil was mixed with water and the suspension was sieved through a 2 mm sieve. Fine roots were collected from the sieve residue and added to the large roots. The roots were oven-dried at 60°C for 72 hours. The dried roots were weighed on a balance to get the RB which was adjusted to g plant^{-1}. Total plant biomass (PB) was the sum of all dry plant material for each genotype including RB and SB harvested from the test plots and recorded in g plant^{-1}. Root to shoot ratio (R/S) was the ratio of the root to shoot biomass as recorded above. Grain yield (GY) was the weight of harvested grain at 12.5% moisture content per genotype per plot and expressed in g plant^{-1}. Harvest index (HI) was also calculated using the following formula:

$$HI = \frac{GY}{Sb} \tag{1}$$

Where HI is the harvest index (%), GY the grain yield (g plant^{-1}), and SB is the shoot biomass (g plant^{-1}).

5.2.3.2 *Carbon analysis*

Due to the exorbitant expenses associated with carbon analysis, a partial analysis was conducted on fifty sorghum and forty-five maize genotypes. For each crop, twenty-five genotypes were meticulously selected based on their grain yield performance and subjected to analysis with two replications. Among these, the top ten and bottom ten performing genotypes were deliberately selected, while five other genotypes were randomly selected. The analysis involved collecting shoot samples to determine shoot carbon content (Scc), root samples for root carbon content (Rcc), and grain samples for grain carbon content (Gcc). These samples were oven dried at 70°C for 48 hours and transformed into fine powder, with each sample weighing 5 grams. The shoots were pulverized into fine powder using a blender, while the roots and grains were processed into fine powder using a ZM 200 ultra centrifugal mill. The total carbon content of the plant, root, and shoot samples was determined by combustion using a LECO TruMac CNS Analyzer.

5.2.3.2.1 *Carbon stocks determination*

The shoot (Scs), root (Rcs), and grain (Gcs) C stocks were defined as the total amount of C measured in the respective plant parts. These C stocks in the two parts were summed up to derive total plant C stocks (Pcs). The carbon stocks were calculated based on the carbon content and corresponding biomasses, utilizing the following formulas:

$$Scs = \frac{Scc}{100} * SB \tag{2}$$

$$Rcs = \frac{Rcc}{100} * RB \tag{3}$$

$$\mathrm{Gcs} = \frac{Gcc}{100} * GY \tag{4}$$

$$Pcs = Scs + Rcs \tag{5}$$

Where Scs is the shoot carbon stock (g $plant^{-1}$), Rcs the root carbon stock (g $plant^{-1}$), Gcs the grain carbon stock (g $plant^{-1}$), Pcs the plant carbon stocks (g $plant^{-1}$), Scc the shoot carbon content (%), Rcc the root carbon content (%), Gcc the grain carbon content (%), SB the shoot biomass (g $plant^{-1}$), RB the root biomass (g $plant^{-1}$), and GY the grain yield (g $plant^{-1}$).

5.2.4 Data analysis

The data collected from the fifty genotypes and twenty-five selected genotypes was analyzed individually. An unbalanced Analysis of variance (ANOVA) was computed to test for genotypes effects on sorghum and maize agronomic performances and carbon storage using Genstat, 20^{th} edition (Payne *et al.,* 2011). Summary statistics, described by mean, median, minimum, maximum, standard deviation (st dev), skewness, 25th quartile (Q1) and 75th quartile (Q3), kurtosis and coefficient of variation were also generated for plant biomass, C stocks, and carbon content variables using Genstat, 20^{th} edition. Correlation coefficients (r), based on Spearman Rank correlations, were carried out using IBM SPSS statistics (Wagner, 2019) to determine the strength of associations between variables.

5.3 Results

5.3.1 *Analysis of variance*

An unbalanced analysis of variance for sorghum and maize showing degrees of freedom, mean square values and significant tests is presented in Table 5.2 and Table 5.3. The unbalanced analysis of variance revealed that the replications were significant only for Scc ($P < 0.05$) in sorghum. There was a significant genetic variation in maize for all the agronomic traits and carbon variables ($P < 0.05$) except for RB, R/S, Rcc, and Gcc. There were significant differences ($P < 0.05$, $P < 0.01$, $P < 0.001$) for all the recorded traits due to blocking except for RB, GY, HI, Rcs, Gcs, and Scc in sorghum. Significant differences ($P < 0.05$, $P < 0.01$, $P < 0.001$) were recorded among test genotypes for GY, HI, Gcs, Scc, Rcc, and Gcc in sorghum.

Table 5.2: Unbalanced Analysis of variance for the twenty-five selected sorghum genotypes and significance tests for agronomic performances and carbon stocks of sorghum

SOV	d.f	PB	SB	RB	R/S	GY	HI	Pcs	Scs	Rcs	Rcs/Rcs	Gcs	Scc	Rcc	Gcc
Replication	1	14.90	17.30	0.10	0.00009	3.33	49.90	7.70	7.20	0.01	0.00003	2.72	1.57*	3.51	0.04
Block	1	5321.30*	5074.30*	2.94	0.26**	0.03	12.00	1050.50*	1027.70*	0.13	0.26**	0.08	0.22	40.22*	0.66***
Genotype	24	1431.60	991.30	51.47	0.02	28.18*	437.50*	291.70	210.20	8.54	0.02	5.45**	0.77*	13.73**	0.65***
Residual	23	964.30	699.50	33.96	0.02	11.62	200.70	194.90	144.70	5.74	0.02	1.71	0.29	8.01	0.01
CV (%)		79.69	81.08	91.8	68.53	69.35	77.58	81.68	82.95	93	68.24	62.22	1.22	6.89	0.27
SE		31.05	26.45	5.83	0.16	3.41	14.17	13.96	12.03	2.4	0.15	1.309	0.54	2.83	0.12

* Significant at P < 0.05, ** P < 0.01, *** P < 0.001, SOV = source of variation, df = degrees of freedom, CV = coefficient of variation, SE standard error, PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, HI= harvest index GY = grain yield, Pcs = total plant carbon stocks, Scs = shoot carbon stock, Rcs = root carbon stock, Rcs/Scs = root to shoot carbon stock ratio, Gcs = grain carbon stock, Scc = shoot carbon content, Rcc = root carbon content, Gcc = grain carbon content.

Table 5.3: Unbalanced Analysis of variance for the twenty-five selected maize genotypes and significance tests for agronomic performances and carbon stocks.

SOV	df	PB	SB	RB	R/S	GY	HI	Pcs	Scs	Rcs	Rcs/Scs	Gcs	Scc	Rcc	Gcc
Replication	1	1247.00	766.00	109.93	0.29	1379.00	220.84	224.80	145.00	17.66	0.28	281.30	0.33	5.70	0.11
Block	2	10560.00*	7433.00*	208.05*	0.14	1596.00	304.76*	1858.80*	1334.00*	30.49	0.18	307.70	1.82*	36.90*	0.23
Genotype	24	416500*	3486.00*	88.17	0.32	2763.00*	203.92*	762.10*	627.40*	18.72	0.40*	546.20*	1.20*	15.49	0.45
Residual	21	1917.00	1532.00	55.78	0.29	1061.00	84.11	350.40	277.60	11.34	0.37	212.10	0.53	10.69	0.33
CV		62.86	76.28	39.87	91.80	64.49	18.28	62.91	76.91	40.78	97.39	64.77	1.72	7.38	1.30
SE		43.79	39.14	7.47	0.54	32.58	9.17	18.72	16.66	3.37	0.60	14.56	0.73	3.27	0.58

* Significant at P < 0.05, ** P < 0.01, *** P < 0.001, SOV = source of variation, df = degrees of freedom, CV = coefficient of variation, SE standard error, PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, HI= harvest index GY = grain yield, Pcs = total plant carbon stocks, Scs = shoot carbon stock, Rcs = root carbon stock, Rcs/Scs = root to shoot carbon stock ratio, Gcs = grain carbon stock, Scc = shoot carbon content, Rcc = root carbon content, Gcc = grain carbon content.

5.3.2 *Agronomic performances and carbon allocation of sorghum lines*

The summary statistics of sorghum and maize agronomic performances and carbon stocks for sorghum and maize genotypes are summarized in Tables 5.4, 5.5, 5.6, and 5.7. Total plant biomass (PB) for sorghum and maize ranged from 14.69 g and 24.29 g of dry matter per plant (g plant^{-1}) to 164.13 g plant^{-1} and 221.10 g plant^{-1}, respectively. The PB mean values for sorghum and maize was 38,24 g plant^{-1} and 71.40 g plant^{-1}; and the median was 31,38 g plant^{-1} and 66.35 g plant^{-1}, respectively. The first quartile for maize and sorghum was at 25.38 g plant^{-1} and 43.80 g plant^{-1}; and the third quartile was at 42.96 g plant^{-1} and 80.79 g plant^{-1}, respectively. The genotypes showed high variation for PB in maize with a standard deviation and variance of 41.95 and 1759.58, respectively. The coefficient of variation of plant biomass was low compared to shoot and root biomass with the value of 63.04% in sorghum. Total plant biomass had the highest positive skewness compared to all the plant parameters with the recorded value 3.34 in sorghum. The SB had the mean of 32.35 g plant^{-1}, with the lowest value of 12,10 g plant^{-1} in sorghum. For sorghum, the mean for SB was 15% lower than the mean for PB. Also, the median for SB was 15% lower than the median for PB with the recorded values of 26.56 g plant^{-1} and 31.38 g plant^{-1}, respectively. The first and third quartile values for SB are 21.09 g plant^{-1} and 35.47 g plant^{-1} in sorghum, respectively. The first and third quartile values for SB were both 17% lower than the first and third values for PB in sorghum. Standard deviation and variance for SB presented small variation between genotypes compared to PB, with the vales of 21.22 and 450.49, respectively (Table 5.4). The coefficient of variation for SB was 4 times greater than the one for PB, with the amount of 65.61%. Shoot biomass portrayed positive skewness with the value of 3.17. Root biomass (RB) had the lowest mean of 5.90 g plant^{-1} compared to all the plant parameters with the value of 0.56 g plant^{-1}. The mean for RB was 81% lower compared to the mean for SB and was 84% lower than that for PB. The median value for RB was 4,45 g plant^{-1}, which was 83% and 86% lower in contrast to SB and PB, respectively (Table 5.4). The first and third quartile had the lowest values of 3.32 g plant^{-1} and 7.33 g plant^{-1} compared to all the plant parameters. The first quartile was 84% and 87% lower compared to the first quartile for SB and PB, respectively. The third quartile was 79% and 83% lower compared to the first quartile for SB and PB, respectively. Standard deviation and variance for RB portrayed very small variation between genotypes compared to SB and PB, with the recorded values of 4.25 and 18.08, respectively. The coefficient of variation for RB is 3 and 9 times greater than that of SB and PB, respectively, with the recorded value of 72,13%. Root biomass portrayed positive skewness with the value of 2.51, which was 21% and 25%

lower compared to SB and PB, respectively. The root to shoot biomass ratio (R/S) ranged from 0.02 to 0.52, with the mean of 0.20. The first and third quartile were at 0.11 g $plant^{-1}$ and 0.23 g $plant^{-1}$, respectively. Very small variation between genotypes was portrayed by R/S with the standard deviation and variance of 0.11 and 0.01, respectively. The coefficient of variation for R/S was 54,96%, with the positive skewness of 0.83. The grain yield ranged from 0.59 g $plant^{-1}$ to 12.88 g $plant^{-1}$, with the mean of 4.79 g $plant^{-1}$. The first and third quartile were at 2.84 g $plant^{-1}$ and 6.36 g $plant^{-1}$, respectively, which was the lowest compared to the quartiles for PB, SB, and RB. The standard deviation and variance for GY portrayed that there is very small variation between genotypes, with the values of 3.05 and 9.31, respectively. The variation between genotypes was the smallest for GY compared to all the plant parameters PB, SB, and RB. The coefficient of variation for GY was 63.70%, which was slightly higher than the coefficient of variation for PB but lower than that of SB and RB. The skewness for GY was the lowest compared to all the plant parameters, with the positive skewness value of 0.85. The harvest index (HI) ranged from 1.52% to 60.23%, with the mean of 17,96%. The first and third quartiles for HI were higher than that for SB, with the values of 7.68% and 24.62%. The variation between genotypes for HI was very small compared to that of SB, with the standard deviation and variance of 175.88 and 73.90, respectively. The coefficient of variation for HI was 73.90%, which was high than that of SB. The skewness for HI was lower than that of SB with positive skewness value of 1.41.

Table 5.4: Summary statistics of the fifty sorghum genotypes for the agronomic traits.

	PB	SB	RB	R/S	GY	HI
Mean	38.24	32.35	5.90	0.20	4.79	17.95
Median	31.38	26.56	4.45	0.19	4.00	14.80
Min	14.69	12.10	0.56	0.02	0.59	1.52
Max	164.13	137.83	26.29	0.52	12.88	60.23
Q1	25.38	21.09	3.32	0.11	2.84	7.68
Q3	42.96	35.47	7.33	0.23	6.36	24.62
st dev	24.11	21.22	4.25	0.11	3.05	13.26
Variance	581.16	450.49	18.08	0.01	9.31	175.88
CV	63.04	65.61	72.13	54.96	63.70	73.90
Skewness	3.24	3.07	2.44	0.81	0.83	1.37
Kurtosis	14.62	12.67	9.38	0.21	0.26	2.11

Min = minimum, Max = maximum, Q1 and Q3 = first and third quartile, st dev = standard deviation, Var = variance, CV = coefficient of variation, PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, GY = grain yield, HI = Harvest index.

Table 5.5: Summary statistics of the forty-five maize genotypes for the agronomic traits.

	PB	SB	RB	R/S	GY	HI
Mean	71.40	50.23	21.52	0.55	44.40	47.32
Median	66.35	43.29	18.67	0.47	41.29	47.15
Min	24.29	12.96	10.67	0.10	5.60	6.81
Max	221.10	202.93	72.00	1.73	172.13	67.53
Q1	43.80	28.40	13.17	0.35	29.72	41.30
Q3	80.79	57.85	23.33	0.60	47.66	55.88
st dev	41.95	35.32	11.32	0.33	28.65	11.90
Variance	1759.58	1247.57	128.10	0.11	820.93	141.70
CV	58.75	70.32	52.60	60.15	64.52	25.16
Skewness	1.90	2.58	2.39	2.02	2.49	-1.07
Kurtosis	4.52	9.05	8.34	4.62	8.99	2.68

Min = minimum, Max = maximum, Q1 and Q3 = first and third quartile, st dev = standard deviation, Var = variance, CV = coefficient of variation, PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, GY = grain yield, HI = Harvest index.

Table 5.6: Summary statistics of the twenty-five selected sorghum genotypes for the agronomic traits and carbon stocks

	PB	SB	RB	R/S	GY	HI	Pcs	Scs	Rcs	Rcs/Scs	Gcs	Scc	Rcc	Gcc
Mean	38.97	32.62	6.35	0.22	5.20	18.84	17.09	14.50	2.59	0.20	2.28	44.18	41.10	43.65
Median	31.50	27.90	4.50	0.19	4.34	12.07	13.76	12.14	1.91	0.17	1.88	44.17	40.55	43.44
Min	14.69	12.10	2.59	0.09	0.59	1.52	6.54	5.41	1.10	0.08	0.26	43.20	33.69	42.89
Max	164.13	137.83	26.29	0.52	12.88	60.23	73.18	62.68	10.50	0.50	5.61	45.48	45.40	45.31
Q1	26.42	21.38	3.64	0.11	1.27	6.20	11.46	9.28	1.48	0.10	0.58	43.73	39.40	43.26
Q3	43.36	35.52	7.11	0.23	8.33	26.03	19.04	15.87	2.80	0.23	3.65	44.56	43.41	44.01
st dev	28.75	24.52	5.08	0.12	4.05	16.45	12.85	11.20	2.04	0.12	1.77	0.61	2.76	0.58
Variance	826.45	601.19	25.79	0.01	16.42	270.44	165.21	125.36	4.15	0.01	3.15	0.38	7.62	0.34
CV	73.77	75.17	79.99	55.22	77.87	87.29	75.23	77.23	78.72	57.36	77.81	1.39	6.72	1.33
Skewness	3.68	3.52	2.84	1.04	0.43	1.19	3.71	3.55	2.79	1.11	0.44	0.35	-0.44	1.37
kurtosis	15.93	14.88	9.71	0.27	-1.23	0.83	16.11	15.08	9.22	0.51	-1.21	-0.81	0.64	1.71

Min = minimum, Max = maximum, Q1 and Q3 = first and third quartile, st dev = standard deviation, Var = variance, CV = coefficient of variation, PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, GY = grain yield, HI = Harvest index, Pcs = total plant carbon stocks, Scs = shoot carbon stock, Rcs = root carbon stock, Rcs/Scs = root to shoot carbon stock ratio, Gcs = grain carbon stock, Scc = shoot carbon content, Rcc = root carbon content, Gcc = grain carbon content.

Table 5.7: Summary statistics of the twenty-five selected maize genotypes for the agronomic traits and carbon stocks.

	PB	SB	RB	R/S	GY	HI	Pcs	Scs	Rcs	Rcs/Scs	Gcs	Scc	Rcc	Gcc
Mean	70.27	51.84	18.64	0.49	49.77	49.46	30.06	21.92	8.23	0.51	22.15	42.30	44.29	44.55
Median	58.79	43.29	17.67	0.43	42.13	51.00	24.46	18.11	7.50	0.42	18.95	42.33	45.70	44.59
Min	24.29	12.96	10.67	0.09	13.11	14.37	10.92	5.58	4.77	0.09	5.77	40.70	35.58	43.82
Max	221.10	202.93	41.00	1.11	185.17	67.53	93.71	85.99	18.82	1.18	81.65	43.92	47.18	45.37
Q1	40.21	21.95	13.00	0.33	23.58	41.60	17.23	9.30	5.87	0.35	10.46	41.84	43.00	44.08
Q3	73.63	54.68	22.00	0.60	55.52	56.21	31.55	23.40	9.88	0.60	24.93	42.79	46.35	44.91
st dev	49.32	44.51	7.35	0.23	38.46	11.36	21.04	18.89	3.29	0.25	17.09	0.81	3.02	0.48
Variance	2432.95	1980.74	53.96	0.06	1479.26	128.94	442.52	356.65	10.84	0.06	292.13	0.66	9.14	0.23
CV	70.20	85.84	39.42	48.32	77.28	22.96	69.99	86.15	40.01	49.93	77.16	1.92	6.83	1.08
Skewness	2.11	2.38	1.58	1.00	2.16	-1.09	2.12	2.39	1.69	1.09	2.12	-0.12	-1.71	0.06
Kurtosis	4.55	6.07	2.82	0.94	5.73	2.55	4.57	6.09	3.48	1.03	5.43	-0.27	2.70	-1.10

Min = minimum, Max = maximum, Q1 and Q3 = first and third quartile, st dev = standard deviation, Var = variance, CV = coefficient of variation, PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, GY = grain yield, HI = Harvest index, Pcs = total plant carbon stocks, Scs = shoot carbon stock, Rcs = root carbon stock, Rcs/Scs = root to shoot carbon stock ratio, Gcs = grain carbon stock, Scc = shoot carbon content, Rcc = root carbon content, Gcc = grain carbon content.

Carbon content variables had the highest means compared to carbon stocks, with more carbon content allocated in the shoots (44.18%) (Table 5.6). Plant carbon stocks for sorghum and maize had the highest mean (17.04 g plant^{-1} and 30.06 g plant^{-1}, respectively) compared to Scs and Rcs. Plant carbon stocks for sorghum and maize had the highest maximum (73.18 g plant^{-1} and 93.71 g plant^{-1}, respectively) compared to all the C variables, followed by Scs (62.68 g plant^{-1} and 85.99 g plant^{-1}, respectively). There was high variation amongst genotypes for Rcs and Gcs compared to all the C variables, with the CV values of 78.72% and 77.81%, respectively (Table 5.6). A minimum Rcs/Scs of 0.08 and 0.09 in sorghum and maize demonstrated that Rcs could be as low as 9% of total plant carbon stocks. There was very low CV for Rcc, Scc, and Gcc, with values of 6.72%, 1.39%, and 1.33%, respectively.

5.3.3 *Mean values for agronomic performances and carbon variables*

The mean performances of sorghum and maize for agronomic traits and carbon variables for the top ten and bottom five genotypes and their rankings for each trait are shown in Table 5.8, 5.9, 5.10, and 5.11. The highest yielding sorghum genotypes were AS115, AS134, AS251, and AS132 with mean yields of 12.88 g plant^{-1}, 12.29 g plant^{-1}, 10.67 g plant^{-1}, and 10.56 g plant^{-1}, respectively (Table 5.8). The highest yielding maize genotypes were TZECOMP3DT/WHITEDTSTRSY-CZ, TZECOMP3 DT-C2, TZ-30, and TZ-44 with mean yields of 172.13 g plant^{-1}, 113.33 g plant^{-1}, 109.68 g plant^{-1}, 72.98 g plant^{-1}, respectively (Table 5.9). Genotype SS27 (8.33 g plant^{-1}) ranked seven for yield production but ranked first for PB, SB, and RB (Table 5.10) with mean values of 164.13 g plant^{-1}, 137.83 g plant^{-1}, and 26.29 g plant^{-1}, respectively. Genotype 9022-13 ranked fifth for both GY and Gcs (Table 5.11). Genotype ranked fifth for SB (78.11 g plant^{-1}) but ranked last for yield production (13.11 g plant^{-1}). As expected, genotype SS27 also ranked first for Pcs, Scs, Rcs, and Scc accumulation with recorded values of 73.81 g plant^{-1}, 62.68 g plant^{-1}, 10.50 g plant^{-1}, and 45.48 g plant^{-1}, respectively. Genotype AS138 ranked second for RB production (13.56 g plant^{-1}) but ranked fourteen for SB production (35.36 g plant^{-1}). Genotype AS251 ranked first for R/S and Rcs/Scs ratios with the mean values of 0.52 and 0.50, respectively. Genotype AS136 ranked forty RB production (3.06 g plant^{-1}) but ranked tenth for yield production (7.50 g plant^{-1}). Genotype AS138 ranked second for Rcs accumulation (5.52 g plant^{-1}) but ranked sixth for yield production (8.54 g plant^{-1}). As expected, all the genotypes that were the top performing for yield production were also the top performing for Gcs accumulation. The genotype that ranked first for yield production but second for Rcc accumulation was AS115 with the mean value of

45.35%. Surprisingly the bottom performing genotypes for yield production AS116, AS563, NW5393, ICSV92001, and AS143 ranked highest for Gcc with mean values of 43.51%, 44.59%, 44.07%, 44.65%, and 44.24%, respectively.

Table 5.8: Mean values of the fifty sorghum genotypes for agronomic traits and carbon stocks.

Genotype	PB	SB	RB	R/S	GY	HI
05-POTCH-138	19.30	15.73	3.57	0.23	4.03	25.64
16MZ	26.42	22.75	3.67	0.16	4.34	19.08
31MZ	36.18	25.73	10.45	0.41	3.18	12.34
AS108	27.08	22.58	4.50	0.20	1.40	6.20
AS109	18.06	14.72	3.34	0.23	3.25	22.07
AS111	18.04	12.92	5.13	0.40	1.25	9.68
AS113	28.40	25.03	3.37	0.13	5.48	21.90
AS114	33.28	26.28	7.00	0.27	3.89	14.80
AS115	25.38	21.38	4.00	0.19	12.88	60.23
AS116	20.15	14.45	5.70	0.39	1.15	7.96
AS117	33.75	27.90	5.85	0.21	1.89	6.77
AS120	68.94	57.84	11.10	0.19		
AS121	38.12	31.97	6.15	0.19	6.23	19.49
AS122	26.63	23.90	2.73	0.11	1.27	5.32
AS129	24.11	22.89	1.22	0.05	3.78	16.50
AS130	39.16	35.52	3.64	0.10	8.81	24.80
AS131	24.69	20.13	4.56	0.23	2.00	9.94
AS132	29.61	22.00	7.61	0.35	10.56	47.98
AS133	31.26	28.50	2.76	0.10	4.47	15.69
AS134	43.36	39.07	4.29	0.11	12.29	31.44
AS135	27.00	24.58	2.42	0.10	2.17	8.81
AS136	31.50	28.44	3.06	0.11	7.50	26.37
AS137	33.93	26.53	7.40	0.28	3.61	13.60
AS138	48.93	35.36	13.56	0.38	8.54	24.14
AS140	23.20	19.24	3.96	0.21	4.70	24.44
AS141	63.63	55.22	8.42	0.15	3.94	7.14
AS143	14.69	12.10	2.59	0.21	0.59	4.84
AS145	32.33	26.58	5.75	0.22	8.21	30.88
AS148	25.40	21.00	4.40	0.21	5.30	25.24
AS203	43.52	31.83	11.69	0.37	8.29	26.03
AS205	101.80	98.50	3.30	0.03	4.00	4.06
AS251	29.67	19.50	10.17	0.52	10.67	54.70

Genotype	PB	SB	RB	R/S	GY	HI
AS391	19.75	17.33	2.42	0.14	4.37	25.18
AS441	35.50	27.00	8.50	0.31		
AS449	23.68	20.69	2.99	0.14	2.50	12.09
AS506	27.89	27.33	0.56	0.02		
AS560	28.58	25.52	3.06	0.12	5.26	20.61
AS563	38.81	35.50	3.31	0.09	1.06	2.99
AS72	37.50	33.92	3.58	0.11	3.38	9.95
AS74	24.37	19.73	4.63	0.23	3.51	17.79
G50	46.50	33.45	13.05	0.39	3.45	10.31
ICS634	67.68	56.25	11.43	0.20	3.89	6.92
ICSV92001	41.79	37.80	3.99	0.11	0.64	1.69
LP4403	30.93	28.20	2.73	0.10	5.88	20.84
MAMOLOKWANE	43.43	39.46	3.96	0.10	4.76	12.07
NW5393	61.99	54.89	7.11	0.13	0.84	1.52
NW5430	21.58	16.08	5.50	0.34	7.35	45.73
PAN8816	60.17	50.67	9.50	0.19	3.75	7.40
SS27	164.13	137.83	26.29	0.19	8.33	6.05
SV07002	50.36	45.57	4.79	0.11	6.50	14.26

PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, GY = grain yield, HI = harvest index.

Table 5.9: Mean values of the forty-five maize genotypes for agronomic traits and carbon stocks.

Genotype	PB	SB	RB	R/S	GY	HI
TZE COMP3DT/WHITE DT STRSYN-CZ	221.10	202.93	18.17	0.10	172.13	47.14
8338-I	41.05	22.39	18.67	1.56	41.63	60.55
9022-13	71.23	54.07	17.17	0.34	67.90	53.05
A21/DT-STR	40.21	25.87	14.33	0.55	19.07	38.87
CKDHL0378	28.94	15.60	13.33	1.24	16.26	50.97
CLHP0343	37.10	24.44	12.67	0.50	43.34	64.05
CML393	123.27	76.60	46.67	0.61	5.60	6.81
CML510	50.00	38.00	12.00	0.31	38.00	42.55
CML540	52.04	38.71	13.33	0.35	48.47	55.75
DT-STR-W-SYN11	50.59	30.93	19.67	0.64	47.47	61.23
DT-STR-W-SYN12	78.34	54.68	23.67	0.44	37.44	39.00
DT-STR-W-SYN13	66.40	32.07	34.33	1.05	41.29	56.00
DT-STR-Y-SYN14	70.63	43.29	27.33	0.64	55.52	56.21
IWDC3 SYN Z1 WHITE DT STR SYN-DTC1	108.14	72.47	35.67	0.49	41.11	34.28
PAN6326R						
PAN6823						

Genotype	PB	SB	RB	R/S	GY	HI
SAMMAZ-16	121.48	86.81	34.67	0.38	42.13	34.35
STR SYN-WI	67.68	48.68	19.00	0.48	41.39	43.32
STR-SYN-YZ	69.45	47.56	21.89	0.46	43.00	47.15
SYN-12	57.12	38.79	18.33	0.47	35.72	47.80
TZECOMP3 DT-C2	58.79	45.79	13.00	0.30	113.33	67.53
T81	101.32	76.98	24.33	0.32	47.49	38.16
TZ COM1/ZDP	56.04	38.38	17.67	0.59	54.70	60.80
TZ-21	66.35	43.68	22.67	0.52	28.56	38.75
TZ-22	57.72	37.05	20.67	0.56	39.03	52.23
TZ-3	153.60	81.60	72.00	0.85	46.08	36.26
TZ-30	205.68	164.68	41.00	0.31	109.68	41.60
TZ-35	45.83	33.16	12.67	0.39	30.88	45.57
TZ-38	34.63	25.29	18.67	0.30	34.39	58.20
TZ-41	41.77	19.77	22.00	1.11	20.43	51.00
TZ-44	83.24	60.58	22.67	0.38	72.98	53.09
TZ-46	90.40	62.73	27.67	0.44	46.00	41.83
TZ-5	34.85	21.85	13.00	0.62	43.62	66.71
TZ-50	100.11	78.11	22.00	0.28	13.11	14.37
TZE COMP5C7/TZE COMP39TCZ	73.63	57.63	16.00	0.36	56.76	51.78
TZECOMP	85.74	58.08	27.67	0.51	47.83	45.10
TZE COMP1-WCB2 WHITEDT STR SYN-D1C1	67.50	44.50	23.00	0.52	34.92	43.58
UK1-2-2	33.88	20.88	13.00	0.63	23.58	53.57
UK1-3	48.55	36.89	11.67	0.37	28.47	43.16
UK1-33	26.28	20.94	10.67	0.24	27.71	56.76
UK1-4	47.58	34.92	12.67	0.37	31.56	46.99
UK1-55	33.29	21.95	11.33	0.54	15.51	41.01
UK1-6	24.29	12.96	11.33	1.73	16.62	59.14
ZDIPLOBC4-C3-W	71.93	54.26	17.67	0.33	50.41	48.93
Z-DIPLO-BC4-C3-W-DTC1	72.60	53.27	19.33	0.36	38.26	39.52

PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, GY = grain yield, HI = harvest index.

Table 5.10: Mean values of the top ten genotypes and five bottom sorghum genotypes for agronomic traits and carbon stocks ranked according to grain yield, with a ranking for each variables

Genotype	PB	PB rank	SB	SB rank	RB	RB rank	RB/SB	R/S rank	GY	GY rank	HI	HI rank	Pcs	Pcs rank	Scs	Scs rank	Rcs	Rcs rank	Rcs/Scs	Rcs/Scs rank	Gcs	Gcs rank	Scc	Scc rank	Rcc	Rcc rank	Gcc	Gcc rank	Mean rank
Top ten genotypes																													
AS115	25.38	**38**	21.38	**37**	4.00	**28**	0.19	**28**	12.88	**1**	60.23	**1**	11.10	**20**	9.28	**19**	1.81	**14**	0.20	**11**	5.61	**1**	43.44	**24**	45.34	**2**	43.56	**9**	**11**
AS134	43.36	**13**	39.07	**10**	4.29	**27**	0.11	**37**	12.29	**2**	31.44	**5**	19.04	**7**	17.35	**5**	1.69	**15**	0.10	**19**	5.31	**2**	44.41	**11**	39.34	**20**	43.25	**18**	**6**
AS251	29.67	**28**	19.50	**42**	10.17	**8**	0.52	**1**	10.67	**3**	54.70	**2**	12.89	**15**	8.57	**21**	4.32	**4**	0.50	**1**	4.59	**3**	43.95	**14**	42.53	**9**	43.06	**22**	**9**
AS132	29.61	**29**	22.00	**36**	7.61	**12**	0.35	**8**	10.56	**4**	47.98	**3**	12.72	**16**	9.79	**18**	2.93	**6**	0.30	**6**	4.56	**4**	44.48	**9**	38.55	**22**	43.16	**21**	**10**
AS130	39.16	**15**	35.52	**12**	3.64	**33**	0.10	**42**	8.81	**5**	24.80	**12**	17.01	**10**	15.53	**9**	1.48	**19**	0.10	**22**	3.82	**5**	43.73	**18**	40.55	**13**	43.40	**14**	**10**
AS138	48.93	**9**	35.36	**14**	13.56	**2**	0.38	**6**	8.54	**6**	24.14	**14**	21.39	**4**	15.87	**8**	5.52	**2**	0.35	**5**	3.70	**6**	44.87	**4**	40.72	**12**	43.36	**15**	**5**
SS27	164.13	**1**	137.83	**1**	26.29	**1**	0.19	**26**	8.33	**7**	6.05	**41**	73.18	**1**	62.68	**1**	10.50	**1**	0.17	**13**	3.61	**7**	45.48	**1**	39.92	**18**	43.27	**17**	**3**
AS203	43.52	**11**	31.83	**18**	11.69	**4**	0.37	**7**	8.29	**8**	26.03	**8**	19.26	**5**	14.18	**10**	5.07	**3**	0.36	**4**	3.60	**8**	44.56	**7**	43.41	**7**	43.47	**11**	**7**
AS145	32.33	**24**	26.58	**25**	5.75	**18**	0.22	**17**	8.21	**9**	30.88	**6**	13.94	**12**	12.01	**14**	1.94	**12**	0.16	**15**			45.16	**2**	33.69	**25**			**12**
AS136	31.50	**25**	28.44	**20**	3.06	**40**	0.11	**38**	7.50	**10**	26.37	**7**	13.76	**13**	12.56	**11**	1.20	**22**	0.10	**21**	3.27	**9**	44.17	**13**	39.15	**21**	43.58	**8**	**13**
Bottom five genotypes																													
AS116	20.15	**45**	14.45	**48**	5.70	**19**	0.39	**4**	1.15	**43**	7.96	**35**	14.38	**22**	12.14	**23**	2.24	**9**	0.18	**3**	0.82	**19**	43.51	**16**	38.33	**16**	43.51	**16**	**23**
AS563	38.81	**16**	35.50	**13**	3.31	**38**	0.09	**47**	1.06	**44**	2.99	**45**	17.20	**9**	15.87	**7**	1.33	**21**	0.08	**25**	0.47	**20**	44.70	**5**	40.26	**15**	44.49	**3**	**20**
NW5393	61.99	**6**	54.89	**6**	7.11	**14**	0.13	**34**	0.84	**45**	1.52	**47**	27.55	**2**	24.75	**2**	2.80	**7**	0.11	**17**	0.37	**21**	45.09	**3**	39.40	**19**	44.07	**5**	**15**
ICSV92001	41.79	**14**	37.80	**11**	3.99	**29**	0.11	**40**	0.64	**46**	1.69	**46**	18.43	**8**	16.84	**6**	1.59	**18**	0.09	**23**	0.28	**22**	44.55	**8**	39.94	**17**	44.65	**2**	**20**
AS143	14.69	**50**	12.10	**50**	2.59	**46**	0.21	**18**	0.59	**47**	4.84	**43**	6.54	**25**	5.41	**25**	1.13	**24**	0.21	**9**	0.26	**23**	44.68	**6**	43.67	**6**	44.24	**4**	**29**

PB = total plant biomass, PB rank = total plant biomass ranking, SB = shoot biomass, SB rank = shoot biomass ranking, RB = root biomass, RB rank = root biomass ranking, R/S = root to ratio, R/S rank = root to shoot ratio ranking, GY = grain yield, GY rank = grain yield ranking, HI = harvest index, HI rank = Harvest index ranking, Pcs = total plant carbon stock, Pcs rank = total plant carbon stock ranking, Scs = shoot carbon stocks, Scs rank = shoot carbon stock ranking, Rcs = root carbon stock, Rcs rank = root carbon stock ranking, Rcs/Scs = root to shoot carbon stock ratio, Rcs/Scs rank = root to shoot carbon stock ratio ranking, Gcs = grain carbon stock, Gcs rank = grain carbon stock ranking, Scc = shoot carbon content, Scc rank = shoot carbon content ranking, Rcc = root carbon content, Rcc rank = root carbon content ranking, Gcc = grain carbon content, Gcc rank= grain carbon content ranking. Mean rank = average rankings for GY, Pcs, Scs, and Rcs. The genotypes are arranged from highest to poor performing based on grain yield.

Table 5.11: Mean values of the top ten genotypes and five bottom maize genotypes for agronomic traits and carbon stocks ranked according to grain yield, with a ranking for each variable.

Genotypes	PB	PB rank	SB	SB rank	RB	RB rank	R/S	R/S rank	GY	GY rank	HI	HI rank	Pcs	Pcs rank	Scs	Scs rank	Rcs	Rcs rank	Rcs/Scs	Rcs/Scs	Gcs	Gcs rank	Scc	Scc rank
Top ten genotypes																								
TZECOMP3DT/WHITEDTSTRSY-CZ	221.10	**1**	202.93	**1**	18.17	**25**	0.10	**43**	172.13	**1**	47.14	**23**	93.71	**1**	85.99	**1**	7.72	**12**	0.09	**25**	81.65	**1**	42.32	**14**
TZECOMP3 DT-C2	58.79	**23**	45.79	**19**	13.00	**33**	0.30	**39**	113.33	**2**	67.53	**1**	24.46	**13**	18.86	**12**	5.60	**21**	0.30	**21**	50.49	**2**	41.53	**20**
TZ-30	205.68	**2**	164.68	**2**	41.00	**3**	0.31	**37**	109.68	**3**	41.60	**32**	88.90	**2**	70.07	**2**	18.82	**1**	0.27	**24**	49.87	**3**	42.36	**12**
TZ-44	83.24	**11**	60.58	**10**	22.67	**13**	0.38	**28**	72.98	**4**	53.09	**14**	35.61	**5**	25.06	**5**	10.55	**5**	0.42	**13**	32.72	**4**	41.28	**22**
9022-13	71.23	**16**	54.07	**15**	17.17	**28**	0.34	**34**	67.90	**5**	53.05	**15**	29.09	**11**	22.90	**9**	6.19	**17**	0.27	**23**	30.03	**5**	42.68	**9**
TZE COMP5C7/TZE COMP39TCZ	73.63	**13**	57.63	**12**	16.00	**29**	0.36	**32**	56.76	**6**	51.78	**17**	31.44	**8**	23.95	**6**	7.50	**13**	0.31	**20**	25.45	**6**	41.21	**23**
DT-STR-Y-SYN14	70.63	**17**	43.29	**22**	27.33	**9**	0.64	**7**	55.52	**7**	56.21	**10**	28.96	**12**	18.11	**13**	10.85	**4**	0.60	**7**	24.93	**7**	41.84	**19**
TZ COM1/ZDP	56.04	**26**	38.38	**25**	17.67	**27**	0.59	**12**	54.70	**8**	60.80	**5**	22.52	**15**	16.11	**15**	6.41	**15**	0.40	**17**	24.37	**8**	41.96	**18**
ZDIPLOBC4-C3-W	71.93	**15**	54.26	**14**	17.67	**26**	0.33	**35**	50.41	**9**	48.93	**20**	31.10	**9**	23.03	**8**	8.08	**11**	0.35	**19**	22.65	**9**	42.57	**11**
CML540	52.04	**27**	38.71	**24**	13.33	**31**	0.35	**33**	48.47	**10**	55.75	**12**	22.61	**14**	16.30	**14**	6.31	**16**	0.39	**18**	21.29	**10**	41.98	**17**
Bottom five genotypes																								
A21/DT-STR	40.21	35	25.87	33	14.33	30	0.55	14	19.07	38	38.87	36	17.23	19	10.59	17	6.64	14	0.63	6	8.42	21	40.94	24
UK1-6	24.29	43	12.96	43	11.33	41	1.73	1	16.62	39	59.14	7	10.92	25	5.58	25	5.34	23	0.96	2	7.50	22	43.07	4
CKDHL0378	28.94	41	15.60	42	13.33	31	1.24	3	16.26	40	50.97	19	12.59	23	6.67	24	5.93	18	0.89	4	7.33	23	42.77	8
UK1-55	33.29	40	21.95	37	11.33	42	0.54	15	15.51	41	41.01	33	14.77	21	9.60	18	5.17	24	0.54	9	6.89	24	43.68	2
TZ-50	100.11	8	78.11	5	22.00	15	0.28	41	13.11	42	14.37	42	44.80	4	34.56	4	10.24	6	0.30	22	5.77	25	43.92	1

PB = total plant biomass, PB rank = total plant biomass ranking, SB = shoot biomass, SB rank = shoot biomass ranking, RB = root biomass, RB rank = root biomass ranking, R/S = root to ratio, R/S rank = root to shoot ratio ranking, GY = grain yield, GY rank = grain yield ranking, HI = harvest index, HI rank = Harvest index ranking, Pcs = total plant carbon stock, Pcs rank = total plant carbon stock ranking, Scs = shoot carbon stocks, Scs rank = shoot carbon stock ranking, Rcs = root carbon stock, Rcs rank = root carbon stock ranking, Rcs/Scs = root to shoot carbon stock ratio, Rcs/Scs rank = root to shoot carbon stock ratio ranking, Gcs = grain carbon stock, Gcs rank = grain carbon stock ranking, Scc = shoot carbon content, Scc rank = shoot carbon content ranking, Rcc = root carbon content, Rcc rank = root carbon content ranking, Gcc = grain carbon content, Gcc rank= grain carbon content ranking. Mean rank = average rankings for GY, Pcs, Scs, and Rcs. The genotypes are arranged from highest to poor performing based on grain yield.

5.3.4 *Correlations between agronomic traits and carbon variables*

Correlation coefficients showing the relationships between agronomic traits and carbon variables for sorghum and maize are shown in Table 5.12 and 5.13. For sorghum total plant biomass had a significant positive correlation with Pcs, Scs, Rcs, and Scc (r = 1.00, 0.95, 0.41, and 0.60, respectively; $P \leq 0.01$) proving a direct link between the C variables. In maize total plant biomass had a significant positive correlation with Pcs, Scs, and Rcs (r = 0.99, 0.97, and 0.77, respectively; $P \leq 0.01$). Shoot biomass was strongly positively correlated with Pcs, Scs, and Scc (r = 0.94, 0.99, and 0.48) compared to root biomass for sorghum. In maize, SB was strongly correlated with Pcs, Scs, Rcs, and Gcs (r = 0.97, 0.91, 0.66, and 0.61, respectively; $P \leq 0.01$). A significant positive correlation for R/S was observed with Rcs and Rcs/Rcs in sorghum (r = 0.63 and 0.96, respectively; $P \leq 0.01$). Shoot carbon stocks had a significant correlation with all the agronomic traits except for RB, GY, and HI in sorghum ($P \leq 0.01$). For sorghum, root to shoot carbon stock ratio displayed a significant correlation with all the agronomic traits except for GY and HI ($P \leq 0.05$ and $P \leq 0.01$, respectively). Grain yield showed higher positive correlations with HI and Gcs in sorghum (r = 0.87 and 1.00, respectively). Harvest index only had significant correlations with Gcs and Gcc in sorghum(r = 0.89 and -0.49, respectively; $P \leq 0.01$ and $P \leq 0.05$, respectively). In sorghum, grain carbon content had a significant negative correlation with grain yield (r = -0.51, $P \leq 0$ .05). Root carbon content had negative correlations with all the agronomic traits and C variables except for R/S, HI, Rcs/Scs, and Gcs with correlation coefficients of 0.15, 0.06, 0.35, and 0.06, respectively, for sorghum.

Table 5.12: Spearman rank correlation of the twenty-five selected sorghum genotypes displaying pair-wise relationship between plant parameters and carbon parameters.

	PB	SB	RB	R/S	GY	HI	Pcs	Scs	Rcs	Rcs/Scs	Gcs	Scc	Rcc	Gcc
PB	1.00													
SB	0.94**	1.00												
RB	0.47*	0.22	1.00											
R/S	-0.35	-0.61**	0.60**	1.00										
GY	0.25	0.15	0.33	0.09	1.00									
HI	-0.10	-0.21	0.16	0.27	0.87**	1.00								
Pcs	1.00**	0.94**	0.48*	-0.35	0.24	-0.12	1.00							
Scs	0.95**	0.99**	0.24	-0.58**	0.14	-0.22	0.95**	1.00						
Rcs	0.41*	0.16	0.98**	0.63**	0.32	0.16	0.41*	0.18	1.00					
Rcs/Scs	-0.44*	-0.67**	0.51**	0.96**	0.13	0.29	-0.44*	-0.65**	0.57**	1.00				
Gcs	0.20	0.09	0.34	0.12	1.00**	0.89**	0.19	0.08	0.36	0.20	1.00			
Scc	0.60**	0.48*	0.40*	0.02	-0.05	-0.21	0.61**	0.51**	0.36	-0.13	-0.12	1.00		
Rcc	-0.53**	-0.51*	-0.29	0.15	-0.05	0.06	-0.52**	-0.50*	-0.16	0.35	0.06	-0.45*	1.00	
Gcc	0.01	0.11	-0.40	-0.44*	-0.51*	-0.49*	0.02	0.12	-0.42*	-0.44*	-0.51*	0.14	0.17	1.00

PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, GY = grain yield, HI = Harvest index, Pcs = total plant carbon stocks, Scs = shoot carbon stock, Rcs = root carbon stock, Rcs/Scs = root to shoot carbon stock ratio, Gcs = grain carbon stock, Scc = shoot carbon content, Rcc = root carbon content, Gcc = grain carbon content. * and ** denote significant at 0.05 and 0.01, respectively.

Table 5.13: Spearman rank correlation of the twenty-five selected maize genotypes displaying pair-wise relationship between plant parameters and carbon parameters.

	PB	SB	RB	R/S	GY	HI	Pcs	Scs	Rcs	Rcs/Scs	Gcs	Scc	Rcc	Gcc
PB	1.00													
SB	0.97**	1.00												
RB	0.77**	0.66**	1.00											
R/S	-0.77**	-0.85**	-0.23	1.00										
GY	0.59**	0.60**	0.32	-0.59**	1.00									
HI	-0.45*	-0.45*	-0.40*	0.29	0.34	1.00								
Pcs	0.99**	0.97**	0.77**	-0.77**	0.55**	-0.49*	1.00							
Scs	0.97**	0.99**	0.64**	-0.85**	0.59**	-0.46*	0.96**	1.00						
Rcs	0.77**	0.66**	0.99**	-0.24	0.26	-0.48*	0.77**	0.64**	1.00					
Rcs/Scs	-0.73**	-0.80**	-0.21	0.97**	-0.63**	0.20	-0.72**	-0.81**	-0.20	1.00				
Gcs	0.59**	0.61**	0.32	-0.60**	0.99**	0.33	0.56**	0.60**	0.27	-0.63**	1.00			
Scc	-0.30	-0.27	-0.31	0.13	-0.49*	-0.12	-0.27	-0.25	-0.33	0.09	-0.50*	1.00		
Rcc	-0.11	-0.07	-0.11	-0.01	-0.31	-0.14	-0.06	-0.09	0.01	0.16	-0.31	0.04	1.00	
Gcc	0.10	0.12	0.03	-0.13	0.06	-0.13	0.09	0.13	0.05	-0.14	0.07	-0.08	0.09	1.00

PB = total plant biomass, SB = shoot biomass, RB = root biomass, R/S = root to shoot ratio, GY = grain yield, HI = Harvest index, Pcs = total plant carbon stocks, Scs = shoot carbon stock, Rcs = root carbon stock, Rcs/Scs = root to shoot carbon stock ratio, Gcs = grain carbon stock, Scc = shoot carbon content, Rcc = root carbon content, Gcc = grain carbon content. * and ** denote significant at 0.05 and 0.01, respectively.

5.4 Discussion

Genotype AS115 and TZECOMP3DT/WHITEDTSTRSY-CZ demonstrated the highest grain yield compared to all other genotypes, possibly due to its higher number of grains per head, likely influenced by their higher shoot biomass (21.38 g plant^{-1} and 202.93 g plant^{-1}) (Table 5.8 and 5.9). This aligns with George-Jaeggli *et al.* (2011) study, which emphasized that seed number is the most crucial yield component associated with increases in sorghum yields. A positive correlation in sorghum was observed between high grain yield and increased shoot biomass and root biomass (Table 5.12), this is consistent with the results reported by George-Jaeggli *et al.* (2011), where increased plant height positively affected grain yield via an effect on shoot biomass. High shoot biomass increases grain production through increasing leaf area for light absorption and carbon assimilation to facilitate grain filling (Reynolds *et al.,* 2005). The positive association in sorghum between root biomass and grain yield demonstrates the significance of root traits in enhancing productivity. Increased root growth improves plant capacity and efficiency in acquiring nutrients and moisture, enhancing agro-ecosystem resilience (Shamuyarira *et al.,* 2022). This is particularly vital under drought conditions when there is less water in the soil profile and a deeper and large root system can forage for water (Figueroa-Bustos *et al.,* 2019). Though larger root systems in crops are beneficial, particularly in arid areas, they may be inefficient or even result in a production penalty in wet seasons or in regions with enough water and capacity to provide additional irrigation. However, evidence from this study suggests that root biomass has positive effects on productivity. These results are consistence with the ones reported by (Fang *et al.,* 2017), who reported that deeper and more profuse root growth can be achieved while maintaining grain production. These larger root diameters can be used to boost soil carbon in agricultural soils. Identification of genotypes based on biomass production and allocation will allow for a more effective explanation of differences between individual genotypes (Cunniff *et al.,* 2015).

Genotypes showed wide variation for agronomic traits and carbon variables, indicating sufficient genetic variation for the development of new sorghum genotypes for grain production and carbon sequestration (Shamuyarira *et al.,* 2022). Phenotypic expression provides an important screening and breeding method to exploit genetic variability. Environmental influences play a significant role in phenotypic variations, and the differential responses of genotypes to environmental conditions contribute to the observed variability (Mutava *et al.,* 2011). The significant variation observed in sorghum and maize biomass and grain yield production among genotypes (Table 5.4 and 5.5) could be attributed to factors such as water availability, sunlight, and susceptibility to weeds and pests. Furthermore, variation in agronomic performances maybe influenced by the amount and distribution of rainfall, leading to adequate moisture and favorable temperature during panicle development and flowering. The harvest index (HI), which indicates the proportion of grain production to above-ground plant biomass, plays a vital role in selecting high-yielding genotypes. A high HI reflects a genotypes ability to efficiently convert biological yield into economic yield (Kusalkar *et al.,* 2003). Genotype AS143 had the lowest grain yield (0.59 g plant^{-1}, Table 5.10) due to low biomass allocation to the roots and shoots. Similarly, genotype AS143 had the lowest HI of 4.84% (Table 5.10). Preventing losses in grain production per plant requires a combination of minimal biomass reduction and an increased HI (George-Jaeggli *et al.,* 2011). Grain yield formation in sorghum and maize is often sink-limited rather than source-limited (Borras *et al.,* 2004).

Genotypes AS115, AS116, and AS143 displayed the lowest accumulation of total plant carbon stocks (Table 5.6), this was associated with their low production of biomass. This is also explained by the positive correlation PB, SB, RB had with Pcs, Scs, and Rcs (Table 5.12). Genotypes SS27, AS138, and AS134 had high biomass, which increased their capacity to sequester more C (Ahmed *et al.,* 2020; Singh *et al.,* 2014). The other genotypes exhibited low C stores because of their low biomass production. In general, all genotypes stored more carbon in their shoots, indicating that roots are weaker C sinks than shoots. Because C is only exported to other sinks when supply exceeds local demand, Scs are higher than Rcs. Root biomass in sorghum showed wide variation in our study. Root biomass ranged from 5.75 to 26.29 g plant^{-1} in several sorghum genotypes (Table 5.4). Another study concluded that root biomass could be an accurate indicator of crop C intake into the soil (Monti and Zatta, 2009). Our findings show that, despite sorghum and maize genotypes allocating less C into their root system than the shoot, certain sorghum genotypes developed more root volume, increasing their competitiveness for nutrients. Similarly, a study hypothesized that less allocation of C to roots, along with a high root length, would result in a higher investment of C in the shoot (Bonifas and Lindquist, 2009). This could explain why numerous sorghum genotypes had high C levels in their shoots in the current investigation.

In sorghum root to shoot ratio (R/S) was negatively correlated with PB, SB, Pcs, and Scs, these results align with the study conducted by Qi *et al.* (2019), who also reported negative correlation between R/S and PB. Brassard *et al.* (2009), reported that the R/S regulates carbon partitioning within shoots and roots. Due to increased carbon allocation to the roots, a higher root-to-shoot ratio may result in significantly less carbon storage in above-ground biomass. Due to the sorghum genotypes genetic make-up, different genotypes may exhibit different R/S. Some genotypes might have evolved to allocate C more efficiently to their roots, influencing C storage patterns (Prasad *et al.,* 2008). Genotype AS116 ranked fourth and third (Table 5.6) for being amongst the genotypes with the highest R/S and Rcs/Scs, respectively, but relatively producing low yields, these results are supported by (Larson *et al.,* 2020) who also reported that if the trade-off oscillates too much towards root development, an excessively high R/S may result in diminished above-ground growth and, eventually, lower grain yields. With PB having the second highest positive correlation with grain yield (Table 5.7), it can be concluded that instead of changing R/S, increasing PB can increase yield without reducing root carbon sequestration capability. It is feasible to increase root and shoot biomass simultaneously to attain high PB, as demonstrated by the positive association between root and shoot biomass (Table 5.7).

Grain carbon content (Gcc) displayed a positive correlation with PB, SB, Scc, Rcc. The high Gcc (Table 5.6) in genotypes ICSV92001, AS563, and NW5393 can be explained by their high production in PB and SB (Table 5.5). These findings are consistent with study reported by (Korner, 2015), who stated that plants accumulate biomass as they grow, which contains carbon. The carbon content of biomass is affected by several factors, including plant species, growth stage, ambient circumstances, and nutrient availability. The more biomass a plant has, the more carbon it contains in general, though the proportion of carbon content can vary. The low Rcc for genotypes AS145 and AS136 could be explained by the negative correlation between Rcc and PB, SB, RB, Pcs, Scs, and Rcs. The carbon content of biomass has a direct impact on the carbon stocks. The more carbon is stored in the plant, the higher the carbon content of the biomass (Keith *et al.,* 2009). Shoot carbon content input was ten times more than the Rcc input. Several sorghum genotypes sequester excessive amounts of C in soil; particularly fine roots may also play a role in soil C sequestration. This study confirmed that some sorghum genotypes can C sink in soil. The amount of C stock in soil by several sorghum genotypes is affected by land-use change and sorghum crop management practices (Tolbert *et al.,* 2002).

5.5 Conclusion

According to the findings, different sorghum and maize genotypes displayed varying carbon sequestration capacities. Some genotypes may have accumulated more carbon in their biomass, implying that certain genotypes have a larger potential for sequestering carbon from the atmosphere. The genotypes that showed the highest potential for carbon sequestration for sorghum were SS27, AS138, AS134, AS203, and AS251; and for maize were TZ-30, TZECOMP3DT/WHITEDTSTRSY-CZ, TZ-44, and TZE COMP5C7/TZE COMP39TCZ, while producing optimum yield and biomass. Several sorghum and maize genotypes offer soil C by increasing root biomass production and root depth. According to the current study, several sorghum and maize genotypes also increased C stock in shoots and roots. These findings support the use of sorghum and maize genotypes to improve soil carbon sequestration. Further research across different environment and test populations is recommended to develop genetic models and guide the selection for breeding of climate-smart sorghum and maize genotypes with high-yielding and high carbon sequestration potential. Understanding the links between biomass, carbon content, and carbon stocks is critical for assessing plant health, investigating carbon cycling in the environment, and assessing the ability of sorghum and maize genotypes to absorb carbon and ameliorate climate change.

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CHAPTER 6: General Discussion

The current project demonstrated significant genetic variation in maize, wheat, and sorghum genotypes for biomass production, grain yield, carbon sequestration and water use efficiency, validating the results of previously funded WRC research (project K5/2721; Water use efficiency and carbon sequestration potential of indigenous crops) that concluded in 2020. Overall, the results from multi-environmental trials confirmed that different crops and cultivars can perform differently in different environments, and this provides key information for making decisions on crop and cultivar selection for a given situation. The findings of the study improve our understanding of the mechanisms responsible for the observed differences in biomass production, grain yield, and water use efficiency of cereal crops, that will be useful in devising strategies for marker-assisted breeding for simultaneous improvement of crops drought tolerance and to enhance climate change mitigation. Several highlights were identified from the project:

- i Maize and sorghum had higher WUE than wheat because the two crops have the C4 photosynthetic system, which is more efficient than the C3 system in wheat. The results also validated that the genotype (G), environment (E) and their interaction (GEI) play an important role in the final expression of biomass production, grain yield, carbon allocation and water use efficiency, suggesting that breeders' quality objectives should be adapted to the targeted environments.
- ii Since crop plants tend to devote more carbon to their shoots than to their roots, sorghum offers the most potential for breeding to improve biomass production. It can also serve as a model crop to increase carbon sequestration. This will significantly lessen the effects of climate change. Maize and wheat will also remain important crops that can be used to support climate smart agriculture.
- iii Direct wheat crosses BW162 × LM75, BW152 × LM75, LM70 × LM75, LM71 × LM75 and LM26 × LM75 and reciprocal crosses LM48 × BW140, LM71 × LM26, LM70 × BW152, LM70 × BW141 and LM75 × LMBW152 are recommended for genetic advancement and cultivar development. The genotypes that showed the highest potential for carbon sequestration for sorghum were SS27, AS138, AS134, AS203, and AS251; and for maize were TZ-30, TZECOMP3DT/WHITEDTSTRSY-CZ, TZ-44, and TZE COMP5C7/TZE COMP39TCZ, while producing optimum yield and biomass. The high root biomass production of all these families and crop cultivars will contribute to carbon inputs through rhizodeposition in agricultural soils, so it is recommended that

the cultivars should be evaluated for net carbon contribution to the soil. In general, further research studies should investigate the link between changes in biomass allocation and atmospheric carbon transfer to soils for improving soil quality and mitigating climate change.

iv With the new wave of renewable energy and bioenergy crops: there is substantial potential that exists to scale up sustainable production of bioenergy from cultivation of high biomass producing cereal and other important crops in southern Africa. A targeted breeding of sorghum for bioenergy production can feed into the drive of expanding biofuel production in a sustainable manner.

Overall, the study identified crop genotypes and newly developed families with high biomass production, grain yield, carbon sequestration and water use efficiency. This is exactly what is demanded by the market and the release of improved cultivars may translate into good value for farmers. These will offer dynamic increase in yield and will be regarded to be the way forward and the first step in a new phase of cultivar development as far as the small grain cultivars in sub-Saharan Africa are concerned. Due to the larger potential of the identified genotypes and developed families, it is recommended that they should be advanced for cultivar development. Nevertheless, we further recommend further research across different and highly diverse environments and test populations to develop genetic models and guide the selection for breeding of climate-smart sorghum, wheat and maize genotypes with high-yielding and high carbon sequestration potential.

Recommendations and Future Research Work

From the overall results of the current study, it is evident that cereal crops had previously been bred for high shoot yield and agronomic value, with below-ground biogeochemical function optimised only due to correlation with yield. Future recommendations are therefore to focus the breeding strategies towards new cultivars with enhanced root systems to improve water efficiency, soil quality and biogeochemical cycling. The development of root-focused cultivars could dramatically and economically reduce atmospheric CO_2 concentrations without decreasing agricultural yields. The goal of future projects should focus on employing high-precision root phenotyping and genotyping to validating root architecture designs and the development of tools for root ideotype design. The future project should also identify quantitative trait loci (QTL) controlling root architecture, genetic markers for this ideotype as well as environmental characteristics highly correlated with phenotypic expression. Finally, these ideotypes should be validated in a representative range of diverse field environments (multiple soil types) with high correlation to predictions from tests done in a small number of fields or in a controlled environment. Development of efficient genomic selection models for root depth can emerge out to have far-reaching impacts in the development of superior high performing, and climate smart crops.

APPENDIXES

CAPACITY DEVELOPMENT

Project WRC 2020/2021-00646's capacity development aimed at harnessing or building individual skills and competencies, especially technical skills, leadership skills, and management skills, on the assumption that more skilled individuals would improve research, development and overall organisational performance. The project also focused on facilitating knowledge exchange for upcoming females and male scientists, members of staff and postgraduate students. To this end, four separate and yet complementary activities were envisaged, namely 1.) national and international online training workshops or webinars, 2.) student supervision, 3.) exchange activities, and 4.) partnerships.

1. One of the flagships of the project "Farming of carbon and water-efficient crop cultivars for climate change mitigation and food security'' https://en.ird.fr/project-cw-farm-farming-carbon-and-water-efficient-crop-cultivars-climate-change-mitigation-and has been instrumental in successfully training of 47 MSc, PhD students and young researchers from different SDEC nationalities in a short on-the job training on "**Mastering Meta-Analysis for water, soil and crop science: A collaborative UNISA, WRC, UKZN, and IRD training workshop**", a workshop that was organized by the Water Research Commission (WRC), Institut de Recherche pour le Dévelopement (IRD), University of South Africa (UNISA) and University of KwaZulu-Natal (UKZN). The workshop was held from the 26th and 27th of August 2021 and was open to students attached to the project and other students who had interests in mastering their skills in meta-analysis. Attached is the expression of interest for the workshop:

EXPRESSION OF INTEREST TO PARTICIPATE IN THE SCIENTIFIC METASHOP – MASTERING THE RESEARCH PROCESS IN META-DATA ANALYSIS – TRAINING ON 26-27 AUGUST 2021
(Training free of charge)

WRC, UNISA, UKZN and IRD have entered a partnership to jointly implement and facilitate water, soil and crop research, in the continent together with other key partners. The activities include knowledge generation and sharing, capacity building, and technology transfer and innovation sharing and co-development.

As a result of this partnership, we are calling for South African and African researchers affiliated with African institutions to consider participating in a free meta-data training that will be held on 26-27 AUGUST 2021. The training will focus on how to retrieve data and develop a review of literature through meta-data analysis while generating new scientific knowledge; how to organise meta-data sets for successful publishing. The main aim is also to provide researchers with skills to meet the primary objective of research and share advice on how to write to successfully publish in high impact journals.

Such systematic process of meta-data analysis for new knowledge generation has been developed by a multidisciplinary and international team of Soil, Water and Crop scientists gathered around a better understanding of the carbon cycle in the soil-plant interface. Over the last 5 years they have published more than 10 meta-papers:

- *Dlamini, P. Chivenge, P., Chaplot, V. 2016. Overgrazing decreases soil organic carbon stocks the most under dry climates and low soil pH: A meta-analysis shows.* ***Agriculture Ecosystems Environment****, 221, 258-269. (Impact factor=5.5*).
- *Mbava, N Mutema, M Zengeni, R Shimelis, H Chaplot V. 2020. Factors affecting crop water use efficiency: A worldwide meta-analysis,* ***AGWAT,*** *228 105878. (IF=4.5).*
- *Mathew, I, Shimelis, H., Mutema, M. Minasny, B., Chaplot V. 2020. Crops for increasing soil organic carbon stocks. A global meta-analysis.* ***Geoderma****. 367. 114230. (IF=6.1).*
- *Dube, HB Mutema, M Muchaonyerwa, P Poesen, J Chaplot V. 2020. A global analysis of the morphology of linear erosion features.* ***Catena*** *190, 104542 (IF=5.2).*

and more recently opinion papers were written based on a critical discussion of these:

- *Chaplot V. 2021. Evidences of plants' impact on land degradation and climate change: An urgent call for new multidisciplinary research.* ***Geoderma*** *392, 114984 (IF=6.1).*
- *Chaplot V and P Smith. 2021. Cropping leads to the loss of soil organic matter: how can we prevent it?* ***SOIL*** *under review (IF=5.8).*

PURPOSE OF WORKSHOP

- Developing academic/ scientific writing skills among postgraduate students/researchers.
- Mentoring/coaching students/researchers to access research papers on their subject, to extract information of interest and to re-organise this information.
- Mentoring/ coaching to analyse meta-data sets.
- Write a journal article based on meta data or own results (prepare a draft plan for further submission to a DHET accredited journal).
- Sharing scientific writing skills, experiences and tips.
- Fostering networking and collaboration opportunities among trainees.

DAY 1 (Thursday 26th August 2021) (SAST)

9:00-10:00	Selecting a suitable research question through Meta data analysis.
10:00-11:00	Searching for research papers. Keys for gathering research papers in a field of interest.
11:00-11:30	Break
11:30-13:00	Building of a data base using classical software.
13:00-14:00	LUNCH
14:00-17:00	Populating the data base with variables of interest.

DAY 2 (Friday 27th August 2021)

09:00-10:00	Our research experiment: how to use the existing literature to make sure we use suitable methodology for acquiring and using data?
10:00-11:00	Data acquisition.
11:00-11:30	Break

11:30-12:30	Quality assessment and data analysis. Data analysis for improved literature study while generating new knowledge.
12:30-13:00	LUNCH
13:00-15:00	Introduction to the plan of a research paper: how to tell the story of our research in an organised way?
15:00-17:00	Building the plan of our own paper; introduction to an 8-week (free of charge) e-course on scientific writing. Working by the trainees.

What should be covered in the Expression of Interest (EoI)?

Applicants should send few words highlighting their current area of interest, broad overview of the relevant project they are involved in and the value that the training will add to their current and future work. The EoI must be submitted via e-mail to Mr Tiyani Chauke at Tiyanic@wrc.org.za before 23 August 2021 at 16:00 SAST. Feedback will be communicated to all applicants by 24 August 2021.

Who is eligible?

The training will be open to all African researchers (including post-graduate students of all levels) with a background in water, but not only limited to it. Participation is free, and the researcher must be affiliated with a legal entity in the continent.

Attendance
Online/virtual

All enquiries and registrations should be directed to Mr Tiyani Chauke at Tiyanic@wrc.org.za.

Following the Meta-Analysis workshop, a **Scientific Writing Course** was conducted from 22 November to 24 December 2021 (free of charge) to interested students and researchers. The objective of the course was to improve the participants' scientific writing skill through a better understanding of the structure of a scientific communication. The activities of the course included:

Exercises to do each week from the structure of an abstract to the writing of a discussion:
- Analysis of scientific articles, selected by the trainees;
- Design of own paper from the identification of the key research questions to specific research objectives; structure of Mat&Meth and results;
- Writing out of document.

2. Three Postgraduate students and one Postdoctoral fellow were trained under the WRC 2020/2021-00646 project, collaboratively supervised by researchers and academics from three institutions: University of South Africa (**Dr Sandiswa Figlan**), University of KwaZulu-Natal (**Prof Hussein Shimelis**) and Institut de Recherche pour le Dévelopement (**Dr Vincent Chaplot**). The students include:

A) Dr Kwame Shamuyarira (graduated with his PhD Plant Breeding from the University of KwaZulu-Natal in 2023 – https://caes.ukzn.ac.za/news/new-breeds-of-wheat-contribute-to-drought-tolerance-and-carbon-sequestration/). The title of his PhD theses was "**Genetic Analysis for Drought Tolerance and Biomass Allocation in Newly Developed Populations of Bread Wheat (*Triticum aestivum*)".**

PhD Thesis Abstract

Bread wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) is the most lucrative commodity crop cultivated worldwide. Wheat productivity is crucial for economic gains and food security to a growing global population. Global wheat production is affected by recurrent droughts that are further exacerbated by a changing climate characterized by rising temperatures and erratic rainfall. In response to these challenges, most wheat breeding has focused on increasing the harvest index to improve grain yield and drought adaptation without considering below-ground root biomass. In recent years there has been a growing interest in using crops such as wheat to store some of the atmospheric carbon previously lost from soils due to past agricultural practices to sustain soil quality and to mitigate against climate change. Increasing biomass allocation of new wheat genotypes to the root system may enhance C extraction from the atmosphere and transfer to crop tissues and to soils through carbon sequestration while increasing resilience to drought stress by improving water and nutrient uptake. Therefore, this study aimed to improve drought tolerance and C sequestration ability of wheat for production under dryland farming systems. The specific objectives of this study were:

i. to provide information based on a retrospective quantitative genetic analysis on combining ability studies of wheat for yield and yield-related traits to predict potential genetic gains achievable in improving biomass allocation for drought tolerance and soil carbon storage;

ii. to determine the extent of genetic variation present in wheat germplasm collections for biomass allocation and drought tolerance based on complementary phenotypic and root attributes and high-density single nucleotide polymorphism (SNP) markers to select breeding parents;

iii. to assess the magnitude of the relationship between root biomass and yield components and to identify influential traits to optimise genotype selection for enhanced biomass allocation, drought tolerance and carbon sequestration potential in bread wheat (Triticum aestivum L.);

iv. to determine the general and specific combining ability, maternal effects and the mode of gene action controlling the major yield-related traits and biomass allocation in wheat to identify good combiners for breeding and enhanced carbon sequestration, and;

v. to determine the genetic variability of newly developed wheat populations for grain yield and biomass allocation under different water stress conditions to select the best-performing families for advancement.

The first study compared data on the general combining ability (GCA) and specific combining ability (SCA) effects of wheat for yield and related traits under optimum and drought-stressed conditions from

40 studies worldwide. Days to heading (DTH), plant height (PH), number of tillers per plant (TN), kernels per spike (KPS), 1,000-kernel weight (TKW), shoot biomass (SB), and grain yield (GY) exhibited wide variation for GCA and SCA effects. Progeny performance increased by 14.30 and 4.04% for SB and GY, respectively, compared with parental values under optimum water conditions. The number of tillers and SB exhibited positive associations with GY ($0.45 \leq r \leq 0.85$, $p < 0.05$) under both water conditions. Meta effect sizes for drought stress were negative. The highest meta-effect sizes were calculated for DTH (−4.5) followed by SB (−2.0), whereas KPS (−1.25) had the lowest. The genetic gains for PH, SB, and other yield components showed that divergent crosses involving complementary parents could enhance biomass allocation patterns in wheat. This could be used as a basis for improving biomass allocation to roots.

In the second study, a total of 97 bread wheat genotypes were evaluated in field and greenhouse trials under drought-stressed and non-stressed conditions and genotyped using 16 382 high-density single nucleotide polymorphism (SNP) markers. The analysis of molecular variance showed that the intrapopulation variance was very high at 99%, with a small minimal inter-population variance (1%). The genetic distance, polymorphic information content and expected heterozygosity varied from 0.20 to 0.88, 0.24 to 1.00 and 0.29 to 0.58, respectively. The cluster analysis based on SNP data showed that 44% and 28% of the assessed genotypes maintained their genetic groups compared to hierarchical clusters under drought-stressed and non-stressed phenotypic data, respectively. The joint analysis using genotypic and phenotypic data resolved three heterotic groups and allowed the selection of genotypes BW140, BW152, BW157, BW162, LM30, LM47, LM48, LM52, LM54 and LM70. The selected genotypes were the most genetically divergent, with high root biomass and grain yield and are recommended for production or breeding.

The third study evaluated 100 wheat genotypes consisting of 10 parents and 90 derived F2 families under drought-stressed and non-stressed conditions at two different sites. Data were collected for DTH, days to maturity (DTM), PH, TN, spike length (SL), spikelets per spike (SPS), KPS, TKW, SB, root biomass (RB), total plant biomass (PB), root-to-shoot ratio (RS) and GY. There was significant ($p < 0.05$) genetic variation in most assessed traits except TN and RS. Root biomass had significant positive correlations with grain yield under drought-stressed ($r = 0.28$) and non-stressed ($r = 0.41$) conditions, but a non-significant correlation was recorded for RS and grain yield. Notably, both root and shoot biomass had significant positive correlations under both water regimes, revealing the potential to increase both traits with minimal biomass trade-offs. The highest positive direct effects on grain yield were found for KPS and PB under both water regimes. The present study demonstrated that selection based on KPS and PB rather than RS will be more effective in ideotype selection of segregating populations for drought tolerance and carbon sequestration potential.

In the fourth study, the above dataset from the ten parental lines and their F2 progeny were subjected to combining ability analysis using a full-diallel mating design. Significant differences were recorded among the tested families revealing substantial variation for PH, KPS, RB, SB, PB and GY. Additive gene effects conditioned PH, SB, PB and GY under drought, suggesting the polygenic inheritance for drought tolerance. Strong maternal and reciprocal genetic effects were recorded for RB across the testing sites under drought-stressed conditions. The parental line LM75 maintained the GCA effects in a positive and desirable direction for SB, PB and GY. Early generation selection using PH, SB, PB and GY will improve drought tolerance by exploiting additive gene action under drought conditions. Higher RB production may be maintained by a positive selection of male and female parents to capture the significant maternal and reciprocal effects found in this study.

The fifth study showed a higher phenotypic coefficient of variation (PCV) than the genotypic coefficient of variation (GCV) for PH, KPS, SB, RB, PB and GY. Moderate heritability of 41.61% and 45.14% and genetic advance as a percentage of the mean (GAM) of 3.49% and 3.58% were observed for RB under drought and for KPS under non-stressed conditions, respectively. Based on correlation and principal component analysis, geometric mean productivity (GMP) and stress tolerance index (STI) were identified as the most efficient drought tolerance indices for selecting drought-tolerant families with high RB. Direct crosses such as BW162 × LM75, BW152 × LM75, LM70 × LM75, LM71 × LM75 and LM26 × LM75 and reciprocal crosses LM48 × BW140, LM71 × LM26, LM70 × BW152, LM70 × BW141 and LM75 × LMBW152 were identified as drought tolerant and are recommended for genetic advancement. The high root biomass production of these families will contribute to carbon inputs through rhizodeposition in agricultural soils. Further research studies should investigate the link between changes in biomass allocation and atmospheric carbon transfer to soils for improving soil quality and mitigating climate change.

The present study revealed that maternal and reciprocal effects should be considered when selecting root biomass and biomass allocation traits. Also, the study identified drought tolerant genotypes and developed new families with high biomass production for enhanced carbon sequestration. The identified families should be advanced for variety development and further evaluated for their net carbon contribution to the soil.

Dr Kwame Shamuyarira is now a lecturer at the University of the Free State. He is now a collaborator in the project and his placement in the Free State is an advantage to the project as it extends our reach in terms of locations that we can use for phenotyping – as this is important in the kind of work that we do. Dr Shamuyarira published the following papers during his PhD work under the project:

a) Shamuyarira, K. W., Shimelis, H., Figlan, S., & Chaplot, V. (2023). Combining ability analysis of yield and biomass allocation related traits in newly developed wheat populations. **Scientific Reports**, 13(1), 11832.

b) Shamuyarira, K. W., Shimelis, H., Figlan, S., & Chaplot, V. (2022). Path coefficient and principal component analyses for biomass allocation, drought tolerance and carbon sequestration potential in wheat. **Plants**, 11(11), 1407.

c) Shamuyarira, K. W., Shimelis, H., Mathew, I., Zengeni, R., & Chaplot, V. (2022). A meta-analysis of combining ability effects in wheat for agronomic traits and drought adaptation: Implications for optimizing biomass allocation. **Crop Science**, 62(1), 139-156.

d) Shamuyarira, K. W., Shimelis, H., Mathew, I., Shayanowako, A., Zengeni, R., & Chaplot, V. (2022). Comparative genetic diversity analysis for biomass allocation and drought tolerance in wheat. **Agronomy**, 12(6), 1457.

Dr Kwame Shamuyarira also presented his work in a local conference and research symposium:

a) Shamuyarira, K. W., Shimelis, H., Figlan, S., & Chaplot, V. 2023. Combining ability analysis of yield and biomass allocation related traits in newly developed wheat populations. Paper delivered at the 2023 Combined Congress, Pretoria, South Africa. 23-26 January 2023.

b) Shamuyarira, K. W., Shimelis, H., Figlan, S., & Chaplot, V. 2023. Path Coefficient and Principal Component Analyses for Biomass Allocation, Drought Tolerance and Carbon Sequestration Potential in Wheat. Postgraduate Research and Innovation Symposium, Durban (Online), South Africa, 8-9 December 2022 (**Best Oral presentation**).

B) Mr Asande Ngidi is due to submit his MSc (Plant Breeding) dissertation in April 2024. He is working on a research project titled **"Estimating Soil Carbon Storage in Maize, Wheat, and Sorghum Genotypes"**, registered with the University of KwaZulu-Natal from 2022-2023.

MSc Dissertation Abstract

Sorghum is a vital food and feed crop in the world's dry regions. It has high biomass production potential for multiple utilities, including in atmospheric carbon (C) sequestration and enriching soil organic matter. Developing sorghum cultivars with high biomass production and carbon sequestration can contribute to soil health and crop productivity. The objective of this study was to assess agronomic performance, biomass production and carbon accumulation in selected sorghum genotypes for production and breeding. Fifty sorghum genotypes were evaluated at three locations (Silverton, Ukulinga, and Bethlehem) in South Africa during 2022 and 2023 growing seasons using a 5 x 10 alpha lattice design with two replications. The following data were collected: days to 50% heading (DTH), days to 50% maturity (DTM), plant height (PH), total plant biomass (PB), shoot biomass (SB), root biomass (RB), root-to-shoot biomass ratio (RS), grain yield (GY), harvest index (HI), grain carbon content (GCc), shoot carbon content (SCc), root carbon content (RCc), total plant carbon stock (PCs), shoot carbon stock (SCs), root carbon stock (RCs), and root-to-shoot carbon stock ratio (RCs/SCs). Significant genotype x location ($P < 0.05$) interactions were detected for most assessed parameters. The highest GY was recorded for genotypes AS115 (25.08 g plant^{-1}), AS251 (21.83 g plant^{-1}), and AS134 (21.42 g plant^{-1}). Genotype AS122 was the top for PB (43.75 g plant^{-1}), ranked second for SB (23.90 g plant^{-1}), and ranked fifth for RB (19.85 g plant^{-1}). Genotypes AS122 and AS27 ranked first and second, respectively, for all the carbon stocks parameters except RCs, whereas genotype AS108 had the highest RCs of 8.87 g plant^{-1}. The highest RS and RCs/SCs were recorded for genotypes AS108 and AS152, with mean values of 1.56 and 3.00, respectively. The principal component analysis (PCA) showed a significant contribution of DTH, PH, PB, SB, RB, and GY correlated with PC1 (with 26.29% explained variance), and PC2 (25.17%). The PCA depicted a positive effect of PCs, SCs, RCs, RCs/SCs, and GCs correlated with PC1 (32.68%) and PC2 (27.68%). The cluster analysis using agronomic and carbon-related parameters delineated the test genotypes into three genetic groups, indicating marked genetic diversity for cultivar development and enhanced C storage and sustainable sorghum production. Further, the study found high root-to-shoot ratio of carbon as a priority trait in estimating carbon sequestration capacity in sorghum. Overall, genotypes such as AS251, SS27, AS134, AS203, and AS563 were selected for their high biomass production, grain yield, and C sequestration potentials. The selected sorghum genotypes are recommended for production or further breeding and variety release adapted to various agro-ecologies in South Africa.

Mr Ngidi has submitted papers for publication

a) Ngidi, A., Shimelis, H., Chaplot, V., Shamuyarira, K.W., & Figlan, S. (2024). Biomass Allocation and Carbon Storage in the Major Cereal Crops: A meta-analysis. Under Review in the Journal of Crop Science.
b) Ngidi, A., Shimelis, H., Abady, S., Figlan, S., & Chaplot, V. (2024). Response of sorghum (Sorghum bicolar [L.] Moench) genotypes for yield and yield components and organic carbon storage in the shoot and root systems. Under Review in Scientific Reports.

Mr Ngidi also presented his work in a local conference and research symposium:

a) Ngidi, A., Shimelis, H., Abady, S., Figlan, S., & Chaplot, V. (2024). Response of sorghum (Sorghum bicolar [L.] Moench) genotypes for yield and yield components and organic carbon storage in the shoot and root systems. Postgraduate Research and innovation Symposium, University of KwaZulu-Natal, 2 & 3 November 2023.

b) Ngidi, A., Shimelis, H., Abady, S., Figlan, S., & Chaplot, V. (2024). Response of sorghum (Sorghum bicolar [L.] Moench) genotypes for yield and yield components and organic carbon storage in the shoot and root systems.

C) **Mr Maltase Mutanda** is registered (2023-2024) for his MSc in Agriculture (Plant Sciences) with the University of South Africa. He is working on a research project titled "**Assessing Water Use Efficiency of Newly Developed Wheat Genotypes under Drought Stress Conditions"**.

MSc Dissertation Abstract

Integrating grain yield, component traits, and metabolite profiles aids in selecting drought-adapted and climate-smart crop varieties preferred by end users. Understanding the trends and magnitude of grain-based metabolites is vital for selecting wheat genotypes with higher grain yield, drought tolerance, water use efficiency, and product profiles. The aim of this study was to determine the response of newly developed wheat genotypes for grain yield and component traits and metabolites under drought stress to guide selection. One hundred wheat genotypes were preliminarily evaluated for agro-morphological traits and water use efficiency under drought-stressed and non-stressed conditions during the 2022 and 2023 growing seasons using a 5 x 20 alpha lattice design with two replications. Ten high-yielding genotypes were selected based on grain yield and were validated for agronomic traits and water use efficiency, and grain samples were assayed to profile their key metabolites under drought. Significant differences existed ($p < 0.05$) among the tested wheat genotypes for yield and yield components, WUE, drought tolerance and major metabolites to discern trait associations. The grain yield of the 10 genotypes ranged from 590.00 g m^{-2} (genotype LM70 X BW140) to 800.00 g m^{-2} (BW141 X LM71) under drought stress, whilst under non-stressed it ranged from 760.06 g m^{-2} (LM70 X BW140) to 908.33 g m^{-2} (LM71 X BW162). Grain yield-based water use efficiency of the assessed genotypes was higher under non-stressed (0.18 g mm^{-1}) than drought stress (0.17 g mm^{-1}) conditions. The highest drought tolerance index (211.67) and stress susceptibility index (0.77) were recorded for BW162 X LM71, whilst the lowest tolerance index (23.33) and stress susceptibility index (0.09) were recorded in BW141 X LM71. Grain metabolites, including the apigenin-8-C-glucoside (log2Fold = 3.00) and malate (log2Fold = 3.60) were present in higher proportions in the high-yielding genotypes (BW141 X LM71 and LM71 X BW162) under drought stress, whilst fructose (log2Fold = -0.50), cellulose (log2Fold = -3.90) showed marked decline in the two genotypes. Based on phenotypic and metabolite profile analyses, genotypes BW141 X LM71 and LM71 X BW162 were selected for being drought-tolerant, water-use efficient, and recommended for production or breeding. The findings revealed associations between yield components, water use efficiency, and grain metabolites to guide the selection of best-performing and drought-tolerant wheat varieties.

Mr Mutanda published the following paper under the project:

a) Mutanda, M., Chaplot, V., Shimelis, H., Shamuyarira, K. W., & Figlan, S. (2024). Determinants of the accuracy of using carbon isotopes in estimating water use efficiency of selected cereal and legume crops: A global perspective. Food and Energy Security, 13(1), e522. https://doi.10.1002/fes3.522

The following paper is under review:

a) Mutanda, M., Figlan, S., Chaplot, V., Madala N.E., Shimelis, H., (2024). Selection of wheat genotypes using yield components, water use efficiency and major metabolites under drought stress. Journal of Agronomy and Crop Science.

Mr Mutanda also presented his work in a local conference and research symposium:

a) Mutanda M, Chaplot V, Shimelis H, Shamuyarira KW, Figlan S. Determinants of the Accuracy of using Carbon Isotopes in Estimating Water Use Efficiency in Selected Cereals and Legumes: A Global Perspective. 2nd Postgraduate Symposium, University of South Africa, 28 June 2023 (**2nd Best Oral presentation**).
b) Mutanda, M., Chaplot, V., Shimelis, H., Shamuyarira, K. W., & Figlan, S. (2024). Determinants of the accuracy of using carbon isotopes in estimating water use efficiency of selected cereal and legume crops: A global perspective. Southern African Plant Breeders Association Conference, Free State South Africa 12 March 2024.

D) An intern in the WRC 2020/2021-00646 project: **Ms Bongeka Lucia Stuurman** graduated with a degree (MSc in Environmental Sciences) at Université Côte d'Azur – Nice, France in 2022, after completing a six-month internship in the project in order to fulfil the requirements for her degree.

E) Dr Isack Mathew served as a Postdoctoral fellow in the project in 2021. Dr Mathew then got permanent employment and started work at LimaGrain in South Africa at the beginning of March 2022, as a maize breeder. His employment was an achievement for the project as it proved the employability of the trainees of the project.
His doctoral research focused on developing larger root systems in wheat to increase drought tolerance and carbon sequestration.

3. The exchange activities sought to enhance technology and knowledge sharing on the underlying plant to soil processes in plant captured C translocation to soils, the associated plant genes for establishing crop breeding strategies and the best management packages for stabilizing soil C.

Researchers from “Institut de Recherche pour le Dévelopement (IRD), Laboratory of Oceanography and Climate, Experiments and Numerical Approaches (LOCEAN)” visited South Africa in 2021 and 2022 (University of South Africa, Science Campus in Florida and the University of KwaZulu-Natal, Scottsville Campus in Pietermaritzburg) and the South African researchers and students also visited France (2022). Overall, the exchange visits imparted several skills and knowledge that will have far-reaching impact on the student's research careers. The project has also exposed the students to the global arena, with the visit to France that took place in December 2022. With three of the South African students having had their first international trip, they understood and appreciated the global efforts towards food security. The summary of the student's reflections from the France trip is below.

FRANCE TRIP (CO-FUNDED BY NRF SA/FRANCE PROTEA BILATERAL GRANT): REFLECTIONS FROM STUDENTS

Kwame Shamuyarira (PhD student)

“The France trip was a great opportunity for us and exposed us not only to the agricultural sector in France but also exposed us to a different culture. We had to adjust to the culturally different way of the French and had to learn and understand their way of leaving. This was very important for our personal development and our ability to work and engage in a world of culturally diverse individuals from different countries.

A major part of the project work that required the presence of Dr Vincent was completed because of the ability to work together in the same setting. We managed to advance our work on using carbon isotopes to estimate for water use efficiency. Our paper on the WUE of sorghum was further developed and is nearing completion. Discussions and planning for future activities was also done efficiently as all project members were in the same setting. This also helped clear up any misunderstandings or confusion in the best way to tackle some of the research problems. This allowed every project member to leave with a clear picture of the objectives and aim of the project.

We visited the university where we learnt on how to measure the different compounds and elements in plant matter. This exposed us to new and advanced equipment that we had not used before. We can use this equipment to analyse our plant and soil samples for carbon content. This also opened our minds to new ideas and research questions that can be pursued in the future in collaboration with French scientists. We had a field trip that was organized for organic farmers. We learnt of the challenges that they face that are unique to organic farming such as challenges with weeds and fertilization, since they are not allowed to use synthetic fertilizers or chemicals. In order to remain profitable, the farmers have to adopt better farming practices including adjusting the timing of organic fertilizer application to suppress weed control. We also learnt that farming in Europe is heavily mechanized and less labour intensive than in South Africa. This makes farming more efficient and some of these technologies can be transferred to South Africa to improve agricultural output from farmers.”

Asande Ngidi (MSc student)

“We went to France on the 23rd of November and came back on the 12th of December. For me it was really a nice experience, and I am very grateful for this opportunity. We were visiting the countryside of France, we got to see Farms (mostly grassland) and most farmers were growing winter wheat, canola, and alfalfa. Also discussed the challenges that they face as wheat farmers, and one of them was perennial weed. They mentioned that it is very difficult to control perennial weeds as they can last for a very long time, and they regrow from roots. We also got to witness how is wheat cleaned and processed to make flour. We also got to spend more time together as students working together. Our supervisor Dr Vincent would come every day in the morning at 08h30 to help us do our work and would guide us and demonstrate to us what is required to reach a certain objective. This trip was very fruitful as we learned that it is more effective to work as a group than as an individual. Dr Vincent focused on one student at a time, and when the student was independent enough, he would proceed to the next student. The only challenged we faced was the weather, it was very cold but were worked through it and made progress. I did data analysis with Dr Vincent and created a table for summary statistics for the sorghum results and did results description and helped me restructure the introduction and the methods and materials for the water use efficiency deliverable. Also visited the Labs at the Sorbonne University Pierre and Marie Curie Campus, and we were shown equipment used for analyzing carbon in plants. Also got to visit Paris, visited the Eiffel tower and the Louvre Pyramid. Also got to learn some French and French culture. I am forever grateful to Dr Sandiswa, Prof Shimelis, Dr Vincent, Unisa, WRC, and NRF for this opportunity. Words cannot express how much of a great experience this was.”

Maltase Mutanda (MSc student)

“Europe houses most of the world's developed countries and a vacation to France was an undeniable opportunity and a dream come true. The interaction with the French wheat farmers was a motivating, educational and empowering experience. I was equipped with the skills to multiply new wheat seed varieties to get adequate seeds for future purposes.

At one point I attended a Wheat Field Day in Epoisses (Countryside in France) where I acquired knowledge on the new ways of producing wheat at a large scale as well as the wheat cultivars that produce high-quality yields. In addition, I was introduced to organic wheat farming which curbs the problems of weeds, pests, and diseases. Above all, I had a wonderful interaction with my supervisors and colleagues, got assistance on doing the meta-analysis database, and got to know and understand the standard of the work I am expected to do. With all gratitude to my supervisors, I am looking forward to analyzing the meta-analysis data, writing a meta-analysis manuscript, and submitting it for publication as soon as possible. Furthermore, traveling to France exposed me to the innovation in French wheat farms. In conclusion, I really enjoyed the vacation, food, visited mesmerizing places, and not forgetting the hospitality I received from Prof Vincent. Indeed, France felt like a home away from home thanks to all my supervisors and vacation organizers for giving us such a wonderful, educational, and team-building experience. It is undeniable that I took home uncountable experiences, and skills and came back with a new boosted energy toward my studies."

Images from the France trip:

4. Strong partnerships were established with the Agricultural Research Council – Agricultural Engineering (**Dr Macdex Mutema**) and the Agricultural Research Council – Small Grain (**Prof Toi Tsilo**).

Overall, the focus of the project on building skills was overtaken by a focus on performance, which held that individuals or organisations would achieve better results once they have developed capacities. The **Principal Investigator** in the project: Dr Sandiswa Figlan, a young and vibrant emerging researcher and has had noteworthy achievements in her research career due to the grooming from the WRC project. She is currently a Project Leader of a number of internally and externally funded research projects, all with a backbone purpose of addressing the agenda of "developing climate smart/resilient crops" in order to "end hunger, achieve food security and improved nutrition, and promote sustainable agriculture" as per the Sustainable Development Goal (SDG) number 2 of the 17 adopted by the UN General Assembly. Her new collaborations resulting from WRC funding are playing a crucial role in strengthening the ties between UNISA and other research-intensive institutes in the African and European continents. Dr Figlan says that "The challenges faced by humanity are not only local but simultaneously global in nature. The challenges do not observe any political, geographic, social or economic boundaries. So, it is imperative to have a multidisciplinary and interdisciplinary research approach and the summoning of the human talent across the globe''. Dr Figlan has therefore strategically placed UNISA in an excellent position to facilitate new dialogues with policy makers and funders across the globe, to identify ground-breaking solutions and create opportunities for investment in the transformation of food systems looking at enhancing food security.

The Co-Principal Investigator in the project: **Dr Vincent Chaplot** is affiliated to both the French Institute for sustainable development (IRD) and the University of KwaZulu-Natal. He is a soil scientist that acquired research expertise over the years, and through working experiences in Europe, America, Asia and Africa on a mixed background of hydrology, agriculture and biology. His expertise has allowed him to investigate issues such as the sustainability of agriculture, ecosystem functioning and adaptation to climate variability, which are major issues in all continents, in a more holistic way. Recent research findings have revealed that when facing nutrient deficiency, plants decompose soil organic matter to mine nutrients, and carbon is released into the atmosphere which causes land degradation, loss of soil water holding capacity and decreased resilience of ecosystems. To complement these findings, Dr Vincent has been involved in collective efforts to better understand the losses of soil carbon by agriculture and their main controls to promote farming practices that will store back some of the lost carbon to soils while using less water for the production of large amounts of food for climate change attenuation and food and water security. The goal of the projects he's been involved in is to anchor such integrated views and research activities into institutes and universities through the building of new teams in which young scientists are trained not only to publish their findings in easily accessible international journals, but also disseminate broadly through getting employed by high level research and education institutions around the world. Dr Chaplot has applauded the students in the project for their hard work and commendable work ethic. He also thanked Dr S Figlan and Prof Shimelis for collaborative efforts in making the project a success.

CONCLUSION

After having identified cultivars with improved ability to restore soils while using less water, the next stage would be to breed these for building the cultivars of tomorrow with enhanced ability to sustainably use agro-ecosystems. A next generation of scientists will have to be also nurtured to acquire the critical skill required for research such as critical thinking and ability to work in teams.