



**GENOTYPIC VARIATION IN WATER USE EFFICIENCY, GASEOUS EXCHANGE AND YIELD OF FOUR CASSAVA LANDRACES GROWN UNDER RAIN-FED CONDITIONS IN SOUTH AFRICA.**

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A dissertation for the degree of Master of Science in Agriculture (Plant Production) in

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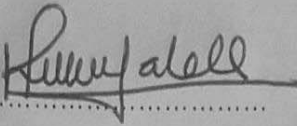
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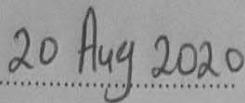
### DECLARATION

I, Kgetise Petros Malele, student number: 11615392, hereby declare that this dissertation for Master of Science in Agriculture (Plant Production) submitted to the Department of Plant Production, School of Agriculture, University of Venda has not been previously submitted for a degree at this or any other University, and that it is my work in design and execution and that all reference material contained therein has been duly acknowledged.

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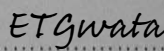
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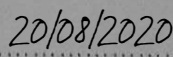
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## **DEDICATION**

I dedicate this work to my aunt **Thandi Joyce Dibakoane** who challenged me to further my studies and for her eternal love, support and encouragement.

## ABSTRACT

Agricultural production under rain-fed conditions is largely dependent on the availability of water stored in the soil during rainfall events. The production of cassava (*Manihot esculenta* Crantz) under rain-fed conditions in the north-eastern part of South Africa is constrained by low and erratic rainfall events. Improving cassava production in the area requires the use of cassava varieties which are efficient in the use of limited soil moisture. The current climate change and increasing population growth on the planet will place more pressure on agriculture to produce more food using less water. Therefore, previously under-researched and underutilised crop like cassava could be used to bridge the food gap in the future. Although the crop currently occupies low levels of utilisation in South Africa and it is cultivated by small-scale farmers in the Low-veld of Mpumalanga, Limpopo and Kwazulu-Natal provinces using landraces with no improved varieties available in the country. Information on the actual pattern of water extraction, water use and water use efficiency of cassava landraces grown in the dry environments of South Africa is limited. Therefore, the objective of the study was to determine the differences in water use efficiency, gaseous exchange and yield among four cassava landraces grown under rain-fed conditions.

Two field experiments were conducted during the wetter (2016/2017) and drier (2017/2018) cropping season at the University of Venda's experimental farm. The trials were laid in a Randomized Complete Block Design (RCBD) consisting of four cassava landraces (ACC#1, ACC#2, ACC#3, and ACC#4) replicated three times. Mature cassava stem cuttings of 30 cm long, were planted manually at a spacing of 1 m x 1 m in both seasons. Each experimental unit consisted of six plant rows of 6 m length (36 m<sup>2</sup>) and 8 rows of 8 m length (64 m<sup>2</sup>) in the 2016/17 and 2017/2018 cropping season, respectively. The experiments were under rain-fed conditions without fertilizer additions and the plots were kept weed-free throughout the experimental period.

Data collected in the field included soil moisture content, gaseous exchange parameters (net leaf CO<sub>2</sub> uptake, stomatal conductance, and intracellular carbon dioxide concentration), chlorophyll content index (CCI), maximum photochemical quantum yield of PSII ( $F_v/F_m$ ), effective quantum yield of PSII ( $\Phi_{PSII}$ ) and photosynthetic active radiation (PAR). Yield and yield components (root length (cm), root girth (cm), number of storage roots and mean root weight (g plant<sup>-1</sup>), root yield and aboveground biomass), as well as water use efficiency (WUE), were determined at harvest. Soil moisture content was measured at seven-day interval from sowing until harvest using a neutron probe. Soil moisture data were used to determine crop water use using the water balance approach.

There was no variation in the root yield and yield components amongst the landraces in 2017/2018 cropping season but, genotypes affected aboveground biomass, root girth, number

of roots per plant and root yield in 2016/2017 cropping season. There was a significant difference ( $P < 0.01$ ) in number of roots (per plant) 81% and 62% greater in ACC#3 and ACC#2 (6.7 & 6.0, respectively) compared with ACC#1 and ACC#4, which both recorded 4 roots per plant. Similarly, root girth was greater in ACC#3 (17.8 cm) and ACC#2 (18.2 cm) compared to ACC#1 (14.1 cm) and ACC#4 (12.9 cm), which were statistically the same. In contrast, total biomass ( $P < 0.01$ ) and root yield ( $P < 0.05$ ) were greater in ACC#3 (20.7 and 11.9 t ha<sup>-1</sup>, respectively) and ACC#1 (22.0 and 11.3 t ha<sup>-1</sup>, respectively) compared to ACC#2 and ACC#4 with root yields of 10.2 and 9.5 t ha<sup>-1</sup>, biomass of 17.1 and 16.3 t ha<sup>-1</sup>, respectively. Although the genotype x cropping season interaction did not affect root yield and yield components, root yield (by 33.8%; 2.7 t ha<sup>-1</sup>) and yield components were greater in the wetter compared to the drier season as expected. Water use efficiency of root yield ( $WUE_{rt}$ ) and water use efficiency of biomass production ( $WUE_b$ ) varied with landraces in season I from 37.0 kg ha<sup>-1</sup> mm<sup>-1</sup> (ACC#4) to 46.60 kg ha<sup>-1</sup> mm<sup>-1</sup> (ACC#3), and between 71.30 kg ha<sup>-1</sup> mm<sup>-1</sup> (ACC#2) and 86.0 kg ha<sup>-1</sup> mm<sup>-1</sup> (ACC#1), respectively.

Landraces did not differ in their water use and soil moisture extraction in both seasons but differed in season. However, there was a significant positive correlation between water use efficiency of root yield ( $WUE_{rt}$ ) (0.963<sup>\*\*\*</sup>) and water use efficiency of biomass production ( $WUE_b$ ) (0.847<sup>\*\*\*</sup>).  $WUE$  of biomass production was greater in the drier than the wetter season partly because of dry matter accumulation per evapotranspiration within the landraces. Photosynthesis did not vary with landraces, however, stomatal conductance varied with landraces from 0.08 mmol m<sup>-2</sup> s<sup>-1</sup> (ACC#4) to 0.2 mmol m<sup>-2</sup> s<sup>-1</sup> (ACC#2). In contrast, ACC#1 and ACC#3 recorded the same value of stomatal conductance, which is 0.1 mmol m<sup>-2</sup> s<sup>-1</sup>. The effective quantum yield of PSII photochemistry ( $\Phi_{PSII}$ ) did not vary with landraces but the maximum photochemical quantum yield of PSII ( $F_v/F_m$ ) varied with landraces from 0.652 (ACC#4) to 0.792 (ACC#3) in season II. The proportion of intercepted radiation was affected by landraces in 2017/2018 cropping season. Highest proportion of intercepted radiation was observed in ACC#3 and the lowest in ACC#2. Proportion of intercepted radiation varied with landraces from 22.62% (ACC#2) to 86.45% (#ACC#3). There were significant genotypic variations in chlorophyll content recorded in both season. Chlorophyll content varied with landraces from 33.1 CCI (ACC4) to 55.4 CCI (#ACC3) in the 2016/2017, and in 2017/2018 cropping season chlorophyll content varied with landraces from 36.9 CCI (ACC4) to 78.7 CCI (#ACC3). The highest genotypic variation in chlorophyll content was observed in ACC#3, whilst the lowest chlorophyll content was recorded in ACC#4 in both seasons.

**Keywords:** Aboveground biomass, cassava, photosynthesis, root yield, water use and water use efficiency.

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## ABBREVIATIONS

(CCI)	Chlorophyll content index
(WUE <sub>b</sub> )	Water use efficiency of biomass production
(WUE <sub>rt</sub> )	Water use efficiency of root yield
ACC	Accession
DAP	Days after planting
E	Transpiration rate
ETR	Electron transfer rate
F <sub>0</sub>	Minimal fluorescence yield of the dark-adapted state F <sub>0</sub> steady-state fluorescence in the light-adapted state
FAO	Food and agriculture organization
F <sub>m</sub>	Maximal fluorescence of the dark-adapted state
F <sub>v</sub> /F <sub>m</sub>	Maximal photochemical quantum yield of PSII
g <sub>s</sub>	Stomatal conductance
iWUE	instantaneous water-use efficiency (=P <sub>n</sub> /E)
MAP	Month after planting
NE	North-eastern
PAR	Photosynthetically active radiation
P <sub>N</sub>	Net photosynthetic rate
PPFD	Photosynthetic photon flux density
PSII	Photosystem II
T <sub>leaf</sub>	Leaf temperature
VPD	Vapour pressure deficit
ΦPSII	Effective quantum yield of PSII photochemistry

## CHAPTER 1: GENERAL INTRODUCTION

### 1.1 Background information

Cassava (*Manihot esculenta Crantz*) is an important perennial food crop that is cultivated mainly for its starchy roots, which are usually harvested from 8 to 36 months after planting (Alves, 2002; Salvador et al., 2014). It is the third most important staple food after maize and rice and provides a rich source of energy for over 800 million people in Africa, Asia and Latin America (Chetty et al., 2013; FAO, 2018; De Souza et al., 2016). Cassava has various uses, for example, the tuberous roots are harvested and used as food for direct human consumption. When processed to remove the inherent cyanogenic glucosides it is used for animal feed, as well as for starch extractions and various industrial purposes (El-Sharkawy, 2016; Fermont et al., 2009; Lebot, 2009). Moreover, starch from the roots is used as a raw material in the textile, paper and the pharmaceutical industries, while the leaves which are rich source of vitamins and proteins are also used as a vegetable (Latif and Müller, 2015).

The available cassava landraces in South Africa have been reported to give a low yield of 8.7 to 15 t ha<sup>-1</sup> (Mathews, 2010; Ogola and Mathews, 2011) when compared to the world average of 28.84 t ha<sup>-1</sup> (FAO, 2018). Problems of water stress that may be attributed largely to the pattern of water extraction, evapotranspiration and the efficiency by which the landraces utilise water have been reported as some of the challenges that need an immediate solution (Mulebeke et al., 2015). Furthermore, the poor biomass accumulation in cassava landraces has also been responsible for low yield even when moisture is not a limiting factor. Whether low yield or biomass accumulation reported in the local landraces is because of low water use efficiency (WUE) or photosynthesis is unclear. However, it has been reported that low WUE and photosynthesis may result in low yield in cassava (Okogbenin et al., 2003) and other crops (Monneveux et al., 2013). Moreover, net photosynthesis in plants is affected by several factors such as gaseous exchange (Rivero et al., 2007; Anjum et al., 2011). Similarly, WUE is affected by dry matter accumulation and photosynthesis. Identification of the local landraces with high photosynthesis and WUE may improve yield and may also help in understanding the causes of low yield in cassava.

High yielding varieties of most crop plants including cassava have been reported to have higher stomatal conductance because of their greater transpiration and water use, (Reynolds et al., 1994; El-Sharkawy, 2016). In contrast, low stomatal conductance because of low transpiration and water use may result in low biomass accumulation. The rate of the cassava plant photosynthesis is affected by environmental conditions on stomatal conductance. Drought

tolerant cultivars will partially close their stomata in response to environmental stresses and internal carbon dioxide concentration at various stages, and this effect is likely to vary with genotypes. Cassava uses a  $C_3$ - $C_4$  intermediate form of photosynthesis on account of high leaf photosynthetic rates (El-Sharkawy and Cock, 1987; El-Sharkawy, 2016).

The partial closures in stomata tend to reduce water loss through transpiration, maximising photosynthesis capacity of the leaf and water use efficiency. Thus, perhaps there is a need to determine the stomatal conductance of the local cassava genotypes and assess its effect on photosynthesis. Furthermore, higher WUE tends to occur when temperature and vapour pressure are low, when the stomatal opening is limited (Itani et al., 1999; Sawatraksa et al., 2018).). This relationship between WUE, vapour pressure deficit (VPD) and stomatal opening in the local landraces has not been reported. Photosynthesis depends on a constant flow of carbon dioxide, gaseous exchange and stomatal opening (Messinger et al., 2006). Poor WUE is induced by stomatal aperture which limits carbon dioxide diffusion into the leaf and subsequently reducing photosynthesis rate and yield (Alves, 2002). WUE may be maximised by increasing the transpiration rate, however, biomass accumulation has been reported to be strongly associated with total transpiration (Fisher and Edmeades, 2010). Therefore, any reduction in transpiration results in a reduction in crop growth rate due to stomatal closure that prevents entry of carbon dioxide hence reduce yield (Morrison et al., 2008). Yield is also a function of the leaf area index and canopy cover.

Whether low yield in cassava has been caused by low photosynthesis rate and capability, poor gaseous exchange or a result of problems in water extraction is not known. Moreover, hardly any study has reported on water use and water use efficiency (WUE) of these landraces. Information on (WUE) is important for accounting for each drop of water that is used to produce yield. WUE is affected by evapotranspiration, and in the local cassava is not known. Therefore, it was hypothesised that cassava landraces, vary in root yield due to differences with respect to gaseous exchange, water use, and water use efficiency when cassava plants are subjected to environmental conditions.

## **1. 2 Objective of the study**

The main objective of the study was to evaluate the differences in water use efficiency, gaseous exchange and yield among four cassava landraces.

The specific objectives of this study were:

- 1.2.1 To determine the difference in gaseous exchange among cassava landraces.
- 1.2.2 To determine the difference in cumulative water use and water use efficiency among cassava landraces.
- 1.2.3 To determine the difference in the pattern of water extraction among cassava landraces.
- 1.2.4 To determine the difference in root yield among cassava landraces.
- 1.2.5 To determine the difference in net photosynthesis rate.
- 1.2.6 To determine the difference in quantum yield of photochemistry II (PSII).



## CHAPTER 2: LITERATURE REVIEW

### 2.1 Cassava production and utilization

Cassava (*Manihot esculenta* Crantz) is also known as manioc, yucca, balinghoy, tapioca or kahoy, tabolchu, mandioca and kappa (Allem, 2002), mutumbula, muthupula, and umjumbula is the third most important source of dietary energy after rice and maize for developing countries of the world (FAO, 2016; Guimarães et al., 2017). The crop belongs in the botanical family *Euphorbiaceae*, tribe *Manihoteae* and genus *Manihot* (Mkumbira, 2002; Nassar, 2005). It grows continuously, having two irregular periods, one for growing and another for storing carbohydrates in its tuberous roots, and these periods are followed by an interval of dormancy (Alves, 2002). Brazil is considered the possible center of origin for this species (Alves, 2002; Souza et al., 2016), being cultivated on 16 million hectares of land worldwide (El-Sharkawy et al., 2008; Guimarães et al., 2017).

It serves as a food security and income generation crop for resource-poor smallholder farmers, particularly in sub-Saharan Africa (Ogola and Mathews, 2011). In Africa, it is the second most important source of energy, and inexpensive food, and emerging cash crop (El-Sharkawy, 2004). Besides being a major staple crop, it serves as an important source of raw material for the starch, feed, and bioethanol industries (Ceballos et al., 2012) for both rural and urban households. Cassava is cultivated in areas considered marginal, where other crops would fail. It is grown where rainfall received per year is limited (from less than 500 mm per year in semi-arid regions to over 2000 mm (El-Sharkawy, 2012). During its growing season, no or little amount of fertilizers is applied (Fermont et al., 2009; El-Sharkawy and De Tafur, 2010). When water is available, cassava maintains a high stomatal conductance with a high internal  $CO_2$  concentration, but when water becomes limiting, the stomata close in response to even small decreases in the soil water potential (El-Sharkawy et al., 1985; El-Sharkawy, 2016). Therefore, cassava can be potentially being considered as a functional staple food crop for small-scale farmers in the dry environments of South Africa.

### 2.2 Cassava production constraints

The cultivation of cassava has been under rain-fed conditions making its performance climate dependent. However, the initiation of climate has made the rainfall pattern more unpredictable thereby affecting crop productivity in the decades to come in dry and semiarid areas like the northeastern part of South Africa (Saxena and John, 2002; Turyagyenda et al., 2013). Cassava cultivation is also affected by several biotic and abiotic stresses that influence negatively on its production and yield (Bull et al., 2011). Its heterozygous nature and long growing cycle have made

breeding new varieties more difficult than other crops (Ceballos et al., 2004). Studies have shown that low yields in cassava have been attributed to the use of late bulking genotypes, low photosynthesis, water use, disease, and pest susceptibility and low yielding potential of many varieties (Nweke, 1996). Pests such as mealy bugs, cassava green mites, whiteflies, grasshoppers and rodents impact negatively on the growth and yield of the crop (Akinbo, 2008). Whiteflies are considered one of the major pests of cassava due to their dual role as direct pests and as a vector for viruses that cause major diseases in cassava (Bellotti and Arias, 2001). The species *Bemisia tabaci* (Bellotti et al., 1999) is the vector of cassava mosaic disease (CMD) caused by *geminiviruses* (Akano et al., 2002; Egesi et al., 2007) with reported yield losses of 20% - 100%. Low water use efficiency and photosynthesis have been observed to cause low yield in cassava (Okogbenin et al., 2003) and on other crops (Monneveux et al., 2013).

### **2.3 Climatic adaptation of cassava**

Cassava requires a warm climate (>20 °C mean day temperature) for optimum growth and production, and maximum leaf photosynthesis with an optimum leaf temperature of 25-35 °C (El-Sharkawy et al., 1992). The crop is often cultivated in the high-altitude tropics (up to 1800 m above sea level) and in the sub-tropics with a lower mean annual temperature where crop growth is slower (Irikura et al., 1979), leaf photosynthetic activities are reduced and storage roots bulking and harvesting time are much delayed compared to what occurs in the warmer climates of the lowland tropics. Temperatures between 16°C and 18°C delay leaf appearance and expansion, which consequently reduce total plant biomass production (Alves, 2002). Within these range of temperatures, there is a delay in sprouting of the stem cutting, and the rate of leaf production, total and storage root are decreased (Cock et al., 1985; El-Sharkawy, 2006) and biomass partitioning into tuberous roots is also reduced, hence yield is reduced (Zhang et al., 2014). Similarly, extended water shortage reduces the rate of leaf formation in all cultivars (Connor and Cock, 1981; Porto, 1983).

Increased temperatures are associated with increased rates of evapotranspiration resulting in a decline in the yield potential of crops (Jiang and Huang, 2001). Studies have shown that yield losses due to the inefficiency of water utilisation tend to vary depending on timing, intensity and duration of the deficit, coupled with other location-specific environmental stress factors such as high irradiance and temperature (Farre and Faci, 2009). Low water use efficiency affects crops through chlorophyll degradation and inhibition of photosynthetic capacity, leading to low yields (Epron and Dreyer, 1993; Jiang and Huang, 2001; Li et al., 2004). A genotype that has greater WUE can maintain its chlorophyll content, as a result, its photosynthesis capacity is maximised.

At high temperatures like the north-eastern region of South Africa, where temperature reaches to 40°C and above in summer a leaf is fully expanded in two weeks and the size increases with plant age up to about four months and then declines; however, at low temperatures the maximum size decreases and is achieved at late growth stages. Leaves produced under prolonged water stress are also smaller, but leaf life or duration of leaf activity increases (Connor and Cock, 1981). Cassava can adapt under variable rain-fed conditions ranging from less than 500 mm per year in semi-arid tropics (De Tafur et al., 1997) to more than 1000 mm in the sub-humid and humid tropics (El-Sharkawy, 2006). Water availability and how it is used is one of the major abiotic constraints to crop production in arid and semi-arid areas such as the north-eastern part of South Africa where rainfall is unpredictable. Research has reported that this region receives an average annual rainfall of about 300-500 mm, with 95% occurring between October and March, often with a mid-season dry spell during critical periods of crop growth, and wide variation from year to year (Bull et al., 2011; Ogola and Mathews, 2011). This indicates that with low, highly variable and unpredictable rainfall coupled with high-temperature regimes in the region may affect production, particularly by small-scale farmers. Therefore, identification of the local landraces with high photosynthesis and WUE is needed and it may create a database for plant breeders for them to choose the desired varieties for further development to improve crop yield of local cassava landraces.

#### **2.4 Genotypic difference in net photosynthesis rate**

Genotypic differences in net photosynthesis in cassava have been reported in several studies. For example, El-Sharkawy (2006), has reported that cassava varieties have high photosynthetic rates. Studies in Colombia have reported cassava maximum leaf photosynthesis of between 42-50  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , as measured in normal air in several field-grown cultivars in favourable environments (El-Sharkawy et al. 1992; El-Sharkawy and De Tafur., 2010). In contrast, for seasonally dry zones, De Tafur et al. (1997) reported a wide range of variation in net leaf photosynthesis among rainfed cassava, as measured in the field during the driest months (Mahon et al., 1977; El-Sharkawy and De Tafur., 2010). The photosynthetic rate ranged from 27 to 31  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , with a significant difference among cultivars. While in semi-arid zones, the photosynthetic rate ranged from 7 to 20  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , also with a significant difference among cultivars (El-Sharkawy et al., 2010). High photosynthetic uptake rates in varieties, may probably due to higher assimilation of carbon dioxide at high rates under high humidity, temperature, high solar radiation and the efficiency by which the genotypes utilise water (El-Sharkawy, 2004) compared to local landraces. High WUE may be a mechanism to increase the

efficiency of resource utilisation ensuring that more carbon is available for growth and biomass production and yield performance.

Photosynthesis rate in cassava ranges from 7 to 50  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  depending on genotype, environmental conditions and the efficiency by which water is used. The variation in net photosynthesis may also be due to the different climates where rainfall patterns, temperature, planting materials, and agronomic practices are different. It is, therefore, necessary to understand the genetic basis of such difference in photosynthesis as well as their relationships with yield to make them useful in a breeding programme particularly under dry environments (Hershey and Jennings 1992, Fukuda et al. 1992; Jennings and Iglesias, 2002).

Net photosynthesis rate of between 7 to 20  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  was also observed in Colombia (E-Sharkawy and De Tafur, 2010). While Alves. (2000) has reported cassava maximum photosynthetic rate varying from 20 to 35  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the field. However, leaf gas exchange rates of field-grown cassava under rain-fed in Nigeria was found to range between 5 and 15  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for most diploids cultivars, 21 and 30  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , for triploids, and 16 and 20  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for tetraploids cultivars, respectively. The high leaf photosynthesis rate indicates the importance of non-stomatal factors (i.e. anatomical and biochemical factors) in controlling carbon assimilation in cassava. As studies showed a strong positive correlation between biomass accumulation and upper canopy net photosynthesis, and negative association with stomatal conductance across a wide range of genotypes, years, and environments (De Tafur et al. 1997, El-Sharkawy 2006).

The genotypic difference in net photosynthesis may be a result of reduced photosynthetic activity, low stomatal conductance and may also leave less water in the soil for photosynthesis than genotypes with high biological activity. Therefore, genotypic variations observed by other researchers in leaf gas exchange characteristics need for more research. Variation in net photosynthesis from various researchers may be due to locations, genotypes and prevailing climate. However, the photosynthetic rate in local cassava varieties in South Africa has not been given any serious scientific attention. It is, therefore, necessary to determine photosynthetic rates in cassava especially in the wake of climate change so that varieties with high photosynthetic and water use efficiencies can be integrated into cassava breeding programmes in South Africa to improve productivity and yield.

## 2.5 Genotypic difference in stomatal conductance among cassava landraces

Genotypic variation in stomatal conductance has been reported in many studies. For example, cassava genotypes have been observed to range between 93 and 391  $\text{mmol m}^{-2} \text{s}^{-1}$ , 440 and 606  $\text{mmol m}^{-2} \text{s}^{-1}$ , respectively (El-Sharkawy, 2007). De Tafur et al. (1997) have reported average stomatal conductance of field-grown cassava cultivars and landraces grown in different locations under rainfed to range between 380 to 590  $\text{mmol m}^{-2} \text{s}^{-1}$  and 370 to 440  $\text{mmol m}^{-2} \text{s}^{-1}$  respectively. Stomatal conductance of cassava varieties with high photosynthesis capacity was found to range between 196 and 391  $\text{mmol m}^{-2} \text{s}^{-1}$  (El-Sharkawy and De Tafur, 2007). In contrast, El-Sharkawy and De Tafur. (2010) have reported stomatal conductance of tall varieties to range from 625 to 769  $\text{mmol m}^{-2} \text{s}^{-1}$  and short varieties were found to range between 588- 833  $\text{mmol m}^{-2} \text{s}^{-1}$ , respectively. A study which was conducted in Nigeria also reported stomatal conductance of cassava genotypes when grown in the field to range between 690 and 860  $\text{mmol m}^{-2} \text{s}^{-1}$  (Allen et al., 2011; Prior et al., 2011; Zhu et al., 2011). Stomatal conductance values seem to be larger than of net photosynthetic rate. This could reflect higher stomatal conductance along the landraces and a more rapid rate of water loss which is needed for photosynthesis (El-Sharkawy and De Tafur, 2010).

It is clearly, showed that variation in stomatal conductance may be due to variation in genotypes, leaf structure, and environmental conditions. Higher leaf temperature ( $42^{\circ}\text{C}$ ) in the afternoon, particularly in the hot climate, causes a reduction in photosynthesis due to lower stomatal conductance and internal carbon dioxide as well as enhanced oxidative stress in cassava (Guerfel et al., 2009). Cassava stomatal control is the major physiological factor that optimises water use under high temperature (Guerfel et al., 2009). Certain genotypes can reduce excessive water loss by closing stomata at high temperatures (Fernandez et al., 1997; Morison et al., 2008). Higher cassava stomatal conductance among the genotypes may be caused by environmental conditions, especially high temperatures which occurs in summer, compared to lower temperatures in winter. Lower temperature delays cassava developments, and reduction of biomass partitioning into tuberous roots, which decreases carbon assimilation hence yield. High leaf conductance may be probably due to greater soil moisture availability in the former season within genotypes. Cassava tend to have higher water use efficiency in summer compared to winter, probably to maximise  $\text{CO}_2$  uptake and minimise water loss.

Research has shown that high yielding cassava varieties have higher stomatal conductance as a result of their greater transpiration and water use (Reynolds et al., 1994). This suggests that higher stomatal conductance results in greater transpiration do leads to greater photosynthesis

and water use (Khanna-Chopra and Sinha, 1988). Cassava water use efficiency and photosynthesis capability is maximised by partial closure of the stomata in response to reduce water loss through transpiration (El-Sharkawy, 2007). Studies have indicated that under optimum conditions, cassava plants generally maintain high stomatal conductance for optimum growth. However, high stomatal conductance does not translate into high root yield. Stomatal conductance is affected by water deficits and it tends to have huge impact of photosynthetic capacity and ultimately storage root yield. However, the impact of water deficit varies among the genotypes and the environments.

Under the dry environment, partial closure of the stomata in response to water loss reduces stomatal conductance, which leads to building up of heat from the metabolic processes. For example, primary metabolites like carbohydrates and sugars which are product of photosynthesis are easily affected by change in leaf characteristics due to build-up of heat. Aspiazu et al. (2010) reported that the closure of stomata by cassava plants prevents the dissipation of heat from metabolic processes such as phenolic which increases leaf temperature. An increase in leaf temperature is caused by high heat indices during the day leading to sunburn on the leaves resulting into an increase in the rate of water loss.

Leaf temperature drops below air temperature when water evaporates making temperature an indirect measure of the instantaneous transpiration at the whole-crop level (Reynolds, 2002). Therefore, breeding for drought sensitive cultivars with desirable traits such as being able to partially have the stomata open during water and temperature stress may be suitable dry environment.

Research has shown that new leaf formation in cassava is often restricted under dry conditions (El-Sharkawy and Cock, 1987; El-Sharkawy, et al., 1992) and therefore selection for higher stomatal conductance should be combined with longer leaf retention (El-Sharkawy, 2004), as the latter trait is positively correlated with productivity (Lenis et al., 2006). Longer leaf retention under water deficit conditions would expose the cassava plant to higher evapotranspiration losses. However, the behaviour of the local cassava when grown in the northeastern region of South Africa has hardly been reported in the literature, hence the need for the study.

## **2.6 The differences in internal carbon dioxide among cassava landraces**

Stomatal opening increases  $CO_2$  diffusion and increases the rate of photosynthesis. According to El-Sharkawy. (2004), the average net intercellular carbon dioxide concentration of field-grown



cassava under rain-fed condition to range between 209 and 295  $\mu\text{molmol}^{-1}$  depending on varieties. Research on genotypic differences in internal carbon dioxide has reported internal carbon dioxide concentration of 179 to 343  $\mu\text{molmol}^{-1}$  when grown in high latitude zones (De Tafur et al., 1997) In contrast, El-Sharkawy (2007) have recorded average internal carbon dioxide concentration of between 233 to 341  $\mu\text{molmol}^{-1}$  under semi-arid environment. While intercellular  $\text{CO}_2$  concentration for some cassava cultivar with high photosynthetic capacity grown on a site with altitude 1 800 m was found to have ranged between 98 and 160  $\mu\text{molmol}^{-1}$ , respectively (El-Sharkawy, 2007).

Cassava is a  $\text{C}_3$  plant based on a number of physiological and biochemical photosynthetic characteristics (Edwards et al., 1990). Genetically, the plant has a  $\text{C}_4$  photosynthetic rate lower than  $\text{C}_3$ . Cassava plant photosynthesis including the  $\text{C}_3$  pathway of photosynthesis rate variation 15-29  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , in normal sunlight and it can reach to a maximum of 40 and 50  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (De Souza et al., 2016)

The relationship between yield and internal carbon dioxide among cultivars is influenced by biochemical factors like enzyme activities. El-Sharkawy (2006) further reported that the leaves of cassava have high activities of  $\text{C}_4$  enzymes and PEP carboxylase but lack anatomy and this may explain why the crop has high photosynthetic efficiency (El-Sharkawy, 2006). Consequently, some studies have suggested that cassava and *Manihot* species are probably evolving biochemically towards the  $\text{C}_4$  photosynthetic pathway with  $\text{C}_3$ - $\text{C}_4$  intermediate behaviour (El-Sharkawy, 2006).

Although cassava is a typical  $\text{C}_3$  plant and thus follows the  $\text{C}_3$  photosynthetic pathway (Ueno and Agarie, 1997). Studies has shown that cassava can assimilate carbon dioxide at high rates under high humidity, temperature and high solar radiation and has also evolved drought tolerance mechanisms similar to  $\text{C}_4$  plants (El-Sharkawy, 2004). Although cassava is tolerant to drought (Onwuene, 2012), higher yield levels are obtained with a larger moisture cycle or with conservation by mulching. Ghuman and Lal (1983) found significantly increase in yield and diameter with higher amount of moisture supply. Cassava (*Manihot esculenta crantz*) responds to decreases in water status by pronounced stomata closure and decreased leaf area growth. Many water deficit responses are thought to be regulated by abscisic acid (Alfredo and Setter 2000). When grown on very poor soils under prolonged drought for more than 6 months, the crop reduces both leaf canopy and transpirational water loss, but the attached leaves remain photosynthetically active, though at greatly reduced rates (Mim, 2003). The main physiological mechanism underlying such a remarkable tolerance to drought was rapid stomatal closure under

both atmospheric and edaphic water stress, protecting the leaf against dehydration while the plant depletes available soil water slowly during long dry periods (Fraser 2007a). This drought tolerance mechanism leads to high crop water use efficiency values (Chang, 1991). Although the cassava fine root system is sparse, compared to other crops, it can penetrate below 2 m soil, thus enabling the crop to exploit deep water if available (EL-Sharkawy, 2004).

However, there are hardly any studies showing the behaviour of internal carbon dioxide on the local landraces when grown in the semiarid of the north-eastern part of South Africa. Indeed, low stomatal conductance may affect photosynthesis and water use, and hence root yields. However, breeding of higher internal carbon dioxide and photosynthesis cultivar may improve the genetic base for efficient water use efficiency in cassava (Hershey and Jennings 1992; Lenis et al., 2006).

## **2.7 The differences in transpiration rate among cassava landraces**

Transpiration and photosynthesis in crops are closely related processes and both are regulated by stomatal activity (Nguyen et al., 1997; Lahai and Ekanayeka, 2010) and are often highly correlated in cassava. Several studies have reported genotypic differences in transpiration rate in field-grown cassava Setter, 2000, 2004; Connor et al., 1981; Connor and Palta, 1981; El-Sharkawy et al., 2010). For example, transpiration rate varied significantly among cultivars, time of day, sites and years. Genotypic difference in transpiration rate of cassava landrace and improved cultivars ranged between 283 and 570  $\mu\text{molmol}^{-1}$  and 264 and 460  $\mu\text{molmol}^{-1}$  respectively.

This means that increased transpiration for the local landraces after midday probably resulted in a water deficit resulting in reduced leaf conductance and  $\text{CO}_2$  exchange. This conclusion also was supported by a significant correlation between leaf conductance and transpiration in other crops (Rajendrudu et al., 1987; Feng et al., 2007). Studies have reported the genotypic variation in the leaf transpiration rate of cassava to range between 115 and 600  $\mu\text{molmol}^{-1}$  (El-Sharkawy, 2007). In contrast, Amurallah et al. (2016) have conducted a study on photosynthesis activity of superior varieties and local varieties and found transpiration rate to a range between 219 and 336  $\mu\text{molmol}^{-1}$ , 397 and 419  $\mu\text{molmol}^{-1}$ , respectively. While transpiration rate of between 136 and 612  $\mu\text{molmol}^{-1}$  was also observed (Lahai and Ekanayeka, 2010). The difference in transpiration rate may be due to stomatal closure and reduce leaf conductivity, impeding photosynthesis which usually ties leaf temperature increases Attridge (1990) because the content of water positively correlated to the rate of photosynthesis. In most water-limited environments, the plant must control water loss and prevent tissue dehydration. Genotypic variation in transpiration rare of cassava genotypes is well documented (Oguntunde 2005; Bergantin et al. 2004; Cruz et al., 2014). However, there is a



dearth of information in the literature on instantaneous transpiration rate behaviour on cassava landraces, especially in dry environments. Most documented studies are cassava whole-plant transpiration (Lahai, 2010) and the instantaneous response may likely vary with genotypes. Information on the transpiration rate may help to understand the low photosynthetic rate, yield and water use efficiency in the local landraces.

## **2.8 The differences in water use efficiency among cassava landraces**

Physiologically, water use efficiency (WUE) is considered as the amount of carbon gained in photosynthesis in exchange for water used in transpiration (Condon et al., 2004). Water use efficiency can also be determined as the relationship between grams of water transpired by a crop per gram of dry matter produced. However, from the agronomists' point of view, WUE is defined as the yield of the harvested product from the water made available (Parry et al., 2005; Monneveux et al., 2013). WUE varies depending on the environment grown. WUE for root yield was reported to range from 20 to 34.38 kg ha<sup>-1</sup> mm<sup>-1</sup> in a tropical climate compared to 10 to 13 kg ha<sup>-1</sup> mm<sup>-1</sup> in a sub-humid temperate climate (Mulebeke et al., 2015; Polthanee and Srisutham, 2018). The performance of genotypes in terms of water use efficiency is strictly based on the conversion of available moisture into dry matter. cassava plants are usually very efficient in using water, that is, they lose less water than many other species, for the fixation of the same amount of carbon dioxide (El-Sharkawy, 2003, 2007).

Such genotypes often have reduced photosynthetic activity, low stomatal conductance and may also leave more water in the soil than genotypes that maintain biological activity (Condon et al., 2002). Stomatal conductance tends to be efficiently regulated under high temperatures to enable water conservation and maximise water use efficiency. Okogbenin et al. (2003) found that cassava genotypes that were more efficient in extracting moisture from deeper soil layers had lower root yield but higher-top growth than those that extracted less water from lower soil layers. The variation in WUE observed between genotypes could be attributed to soil moisture characteristics, although the growth and physiological characteristics of the crop could be considered. The material that constitutes the yield could partially contribute to the difference i.e. root tuber in cassava compared to other crops (Steduto et al., 2007). This means that the extracted water was lost through evapotranspiration, which resulted in low yield. Water use efficiency in cassava tend to differ with genotype, studies have shown that can partially stomatal closure reduce excessive water loss through transpiration. Genotypes that have slower stomatal conductance tend to deplete all the stored water due to low carbon dioxide uptake and higher water loss.

Drought escape is defined as the ability of a plant to complete its life cycle before serious soil and plant water deficits occur (Bakayoko et al., 2009). It involves rapid phenological development developmental plasticity (variation in duration of growth period depending on the extent of water-deficit) and remobilization of assimilates to grain in the case of cereals. Under low soil water conditions, plants enhance their ability for improved water uptake through extending the rooting system and increasing root length density, cm root per cm soil (Ahmadi et al., 2011). Soil water distribution, soil texture, and soil structure have major effects on root growth and distribution (Wang et al., 2006).

Drought avoidance is the ability of plants to maintain relatively high tissue water potential despite a shortage of soil-moisture (Beebe et al., 2013). Drought avoidance is achieved by maintenance of turgor through increased rooting depth, efficient root systems and increased hydraulic conductance and by reduction of water loss through reduced epidermal conductance, reduced absorption of radiation by leaf rolling or folding (Ahmadi et al., 2011) and reduced evaporation surface (Polthanee and Srisutham (2017). Plants under drought condition survive by doing a balancing act between maintenance of turgor and reduction of water loss (Shashidhar et al., 2000).

Drought tolerance is the ability to withstand water-deficit with low tissue water potential (Beebe et al., 2013). The mechanisms of drought tolerance include maintenance of turgor through osmotic adjustment, increase in elasticity in cells and decrease in cell size and desiccation by protoplasmic resistance (Ugherughe, 1986). The mechanisms that confer drought tolerance by reducing water loss (such as stomatal closure and reduced leaf area) usually result in reduced assimilation of carbon dioxide (El-Sharkway, 2006). Osmotic adjustment increases drought resistance by maintaining plant turgor, but the increased solute concentration responsible for osmotic adjustment may have detrimental effects in addition to energy requirements for osmotic adjustment. Premachandra et al. (1994) and Sanchez et al. (2001) reported that certain traits that confer tolerance and survival under drought conditions are often associated with reduced photosynthesis and yield potential. It is therefore necessary to understand the genetic basis of such traits as well as their relationships with yield to make them useful in a breeding programme. Crops must balance the mechanisms of escape, avoidance and tolerance in order to be productive (Blum, 2011).

Cassava tends to maximise water-use efficiency through a reduction in transpiration (Blum, 2005; Blum, 2009). Blum (2005) have reported that high WUE is a function of reduced water use and does not necessarily mean an improvement in plant productivity. This implies that indiscriminate

selection for higher WUE with the assumption that it equates with improved yield under dry conditions might not result in the desired expectation. Dry matter production is strongly associated with total transpiration, therefore any reduction in transpiration results in reduced crop growth rate (Udayakumar et al., 1998). Stomatal closure ensures moisture conservation but also have a negative influence on crop productivity, because it prevents entry of carbon dioxide into the leaves, increases evapotranspiration and reducing yield (Morrison et al., 2008).

However, there is a need for further studies to ascertain the contribution of physiological factors such as photosynthesis and chlorophyll fluorescence on this difference. There is also a need to take measures to maintain soil moisture and improve water use efficiency in dryland cropping systems like Venda. This indicates that conditions that increase soil moisture content and reduce evapotranspiration and high relative humidity tend to increase water use and vice versa. This likely contributed to the higher water use efficiency and root yield of plants in 2016/2017 cropping season with high rainfall and reduced evapotranspiration rate than in 2017/2018 cropping season. There is hardly any published literature on the actual pattern of water extraction and the efficiency by which the local landraces utilise water when grown in the northeastern region of South Africa. The selection of landraces with greater water use may improve both WUE of root yield and biomass production for cassava.

## **2.9 The difference in chlorophyll content among cassava landraces**

Chlorophyll is the primary light receptor in the leaf of cassava. It consists of pigment which is important for the absorption of solar radiation. Thus, from a physiological perspective, leaf chlorophyll content is, therefore, a significant parameter in photosynthesis that needs to be investigated in the cassava local landraces. Filella et al. (1995) have independently reported that low concentrations of chlorophyll can directly limit photosynthetic potential and hence yield. There is a close relationship between chlorophyll concentration, leaf nitrogen content and crop yield (Cartelat et al., 2005). This relationship arises because the majority of leaf nitrogen is usually contained in chlorophyll (Cartelat et al., 2005). Since chlorophyll absorbs photosynthetic active radiation (PAR), which aids in photosynthesis, it indicates the strength of the internal leaf apparatus during photosynthesis (Li et al., 2006). Leaf chlorophyll content can be determined by extraction with organic solvents including acetone (Liu et al., 2008) and methanol (Cenkci et al., 2010) and subsequent quantification using a spectrometer; however, this method is expensive and time-consuming (Jangpromma et al., 2010). A higher throughput non-destructive method is the SPAD chlorophyll meter that allows rapid and inexpensive assessment of leaf greenness (Ahmed, 2011). SPAD measures leaf absorbance in the red (650 nm) and infrared (940 nm)

regions (Markwell et al., 1995), and gives readings that have been correlated with chlorophyll content under different moisture regimes in cassava and many crops (Jangpromma et al., 2010).

Several studies have reported on the genotypic variation in chlorophyll content of cassava crop (Jiang and Huang, 2001; Colom and Vazzana, 2003; Li et al., 2004; Paknejad et al., 2007; De Souza et al., 2016). For example, there was variation in chlorophyll content of cassava cultivars as compared to four other local varieties but has a density of stomata narrowest tenuous invitation, otherwise, cassava varieties while other varieties generate total chlorophyll content of at least ( $0.95 \mu\text{g g}^{-1}$ ) but it has the most stomata and meetings. Cassava varieties that produce enough chlorophyll content and density of stomata were observed to have the widest stomata (Ayanru and Sharman, 1981). Leaf temperature has great effect on water vapour concentration within a leaf and thus on transpiration, and in general stomata open more widely as temperature increases (Lahai and Ekanayake, 2009). Increase in leaf temperature increased transpiration, which most likely reduced water use in the study.

Leaf chlorophyll content directly affects the transmission and distribution of energy absorption of light and the photosynthetic efficiency is directly affected by photosynthetic leaf (Lin et al., 1992; Hou et al., 2013).

The difference in chlorophyll content among the genotypes may also be because of less light being absorbed and more transmitted due to reduced specific leaf area. Several studies have shown that reduction in chlorophyll content occurs because of poor utilisation of water by the cassava thereby inhibiting their photosynthetic capacity (Jiang and Huang, 2001; Colom and Vazzana, 2003; Li et al., 2004) and hence function (Epron and Dreyer, 1993). The difference in chlorophyll content may originate at the level of the photosynthetic machinery (Malkin and Fork, 1981). One of the possible factors which contribute to the difference amongst the genotype may be the ratio of antennae chlorophyll to the reaction centre (Arunyanark et al., 2008).

Although root yield in cassava genotypes increased with an increase in the concentration of three-leaf chlorophyll components (a, b and ab) under limited moisture (Lahai et al., 2003), little has been done to exploit the genetic variation in cassava chlorophyll content. The response in chlorophyll content may vary with genotypes. Studies have indicated that yield advancement is expected since cassava genotypes that maintained their chlorophyll content under dry areas like Venda which tend to give much higher yield and water use efficiency than other genotypes (Byju and Haripriya-Anand, 2009). Hardly any study has been done to assess chlorophyll content of cassava under the rain-fed dry condition of Limpopo, hence there is a need to investigate it.

## 2.10 The difference in quantum yield of PSII among cassava landraces

Photosynthesis is light energy driven which synthesizes carbohydrates from carbon dioxide and water with the generation of oxygen. Crop productivity is associated with the ability of photosynthesis. Chlorophyll is the principal light receptor in the leaf of a plant. It consists of chlorophylls a (Chl a) and chlorophylls b (Chl b) and together with other antenna pigment are the most important pigments for light receptors. These pigments absorb solar radiation, and through resonance transfer, emit the light energy to the reaction center pigments, which release electrons and set in motion the photochemical process. Thus, from physiological perspective, leaf chlorophyll content is therefore a significant parameter in photosynthesis that needs to be investigated (Richardson et al., 2002).

Depending on the status of photosynthetic apparatus, a certain amount of light energy absorbed by chlorophyll molecules can undergo other processes except photochemistry, such as dissipation as heat or as chlorophyll fluorescence. Maximum quantum yield of PSII measured in light-adapted leaves is a sensitive indicator of photosynthetic performance, with optimal values of around 0.83 measured from cassava plant (Maxwell and Johnson, 2000).

Photoinhibition may lead to damage to chlorophyll molecules (Souza et al., 2004) and may inactivate PSII enzymes resulting in decreased carbon assimilation as demonstrated previously (Colom and Vazzana, 2003). Lower leaf surface area in the sun compared to shade leaves may assist in increasing water use efficiency by conserving water lost through transpiration. However, Calatayud et al. (2000) have also reported a cassava quantum yield of 0.80. Genotypic differences were observed for quantum yield and were found to range between 0.71 to 0.84 under non-stressed and 0.55 to 0.78 under cold-stress conditions (Togun et al., 2004). In contrast, the influence of water and heat stress affected maximum quantum yield of PSII photochemistry and its value was between 0.69 and 0.80. The typical range for the maximum quantum yield of PSII among vascular plants is 0.75–0.85 for no stressed plants and values below 0.75 indicate a stressful situation (Björkman and Demmig, 1987; Bolh ar-Nordenkampf et al., 1989). High chlorophyll fluorescence values indicate high quantum efficiency of photochemistry and heat dissipation that increase crop photosynthesis and biomass (El-Sharkawy and De Tafur, 2010; Murchie and Lawson, 2013).

The difference in quantum yield among cassava varieties indicates differences in their genotypic response to adjust stressed conditions were lower than those under well to varying light intensities and temperatures. Thus, chlorophyll fluorescence could be a useful tool in screening for water and heat stress in cassava to enhance crop productivity and yields. However, under a high latitude

environment hardly any published literature has reported the behaviour of quantum yield of cassava in the northeastern part of South Africa.

### **2.11 The difference in yield among cassava landraces**

Variation in yield among cassava genotypes has been studied by numerous researchers, and studies show root yield may be improved through genotype selection and manipulation of management practices. Studies have reported root yield of cassava genotypes to range from 31.17 to 56.17 t ha<sup>-1</sup> when grown in the dry and semiarid of Colombia (El-Sharkawy, 2007). Significant differences in root yield were observed for genotypes at the different harvesting times under irrigation and rain-fed. The highest root yield at 10 MAP was 25.67 t ha<sup>-1</sup> under irrigation was obtained from variety 00/0203 while CTSIA 48 had the lowest root yield (12.08 t ha<sup>-1</sup>). Under rain-fed condition, cultivar 96/1708 had the highest root yield of 19.67 t ha<sup>-1</sup> whilst CTSIA 48 had the lowest (11.42 t ha<sup>-1</sup>) at 10 MAP. While average root yields at 12 MAP were 16.39 and 26.58 t ha<sup>-1</sup> under rain-fed and irrigation, respectively. The difference in root yield among the genotypes may be due to the rate of accumulation of dry matter into the roots also variation in water use. Cassava low yield under rain-fed condition might have been caused by the decrease in stomatal conductance due to the closure of stomata under water deficit. Cassava plants rapidly closed their stomata under stress to reduce water loss and maximise water use but this inhibits photosynthetic activity (El-Sharkawy, 2007).

Genotypic variation in root yields in the different environments, from one year to the other. The highest root yield at Fumesua in 2013 was obtained from MM96/1751 (45.9 t ha<sup>-1</sup>) with the lowest yield coming from CTSIA 110 (9.46 t ha<sup>-1</sup>). Average root yield for all genotypes across environments was 24.79 t ha<sup>-1</sup>. UCC2001/449 had the highest overall root yield of 34.09 t ha<sup>-1</sup> with CTSIA 65 having the lowest root yield 14.24 t ha<sup>-1</sup> (Fisher and Edmeades, 2010).

Ogola and Matthew, (2011) have reported genotypic differences in cassava root yield of 6 and 12 MAP (38.4 and 52.7 t ha<sup>-1</sup>, respectively. This implies that such genotypes continuously accumulated dry matter even during the stress periods. Those that had low root yield at six months might have used the above-ground part as the major sink before accumulating some into storage roots. El-Sharkawy (2004) stated that the distribution of carbohydrates to the different organs of cassava changes during the growth cycle, with the shoot being the major sink during the first five months while storage roots become the major sink later. Previous studies by Adjebeng-Danquah et al. (2012) indicated that genotypes that partitioned earlier dry matter production into storage roots were able to bulk over 60 percent of their final root yield by six months after planting. It is noteworthy that cassava may be well adapted to the dry environments of the Limpopo river basin



that experience terminal drought and low mid-season temperatures. Root yield is influenced by environmental conditions and genotypes as shown by the strong genotype x environment interaction. Certain genotypes were found to have high and stable root yield across environments. It can be concluded that the significant genotype-environment interaction in root yield and yield components makes it difficult to select one genotype for all environments. Among the major constraints affecting crop production are low photosynthesis, water use, and unpredictable rainfall. Drought severely impairs plant growth, development, and plant production more than any other environmental factor (Shao et al., 2009). Under rain-fed conditions, major challenges facing farmers in dry and semiarid zones of the world are lack of inputs, water, pest and diseases which causes low yields in cassava (Okogbenin et al., 2003; El-Sharkawy, 2007). However, very little work has been done in the north-eastern region of South Africa to evaluate water use and the efficiency by which the locals utilize water that is why there is low yield of local landraces compared to the world average. Studies have shown that WUE is an important determinant of yield under water stress conditions and even as a component of crop drought resistance (Blum, 2005). This suggests that rain-fed crop production can be increased per unit water used, resulting in greater water use efficiency (Kijne et al., 2003).

### **2.12 Photosynthetically active radiation (PAR)**

The photosynthetic active radiation spectrum (PAR), which makes up 50% of the total global radiation (Bonhomme, 2000), lies in the wavelength 400 – 700 nm (Zhang et al., 2008). The crop canopy absorbs PAR, referred to as intercepted photosynthetically active radiation (IPAR) which is intercepted light used for photosynthesis and eventually producing plant biomass (Johnson et al., 2010). The radiation intercepted during the growing period is determined by the canopy radiation extinction coefficient ( $k$ ) and is influenced by leaf orientation and the green leaf area (Thomson and Siddique, 1997).

Research has shown that lower  $k$  values are associated with narrow and erect leaves compared to plant genotypes with more horizontal leaf arrangements (Kiniry et al., 2005). Lower  $k$  values allow light to penetrate the canopy and illuminate more leaf area in conditions of low light intensity, thus increasing carbon exchange rates, and consequently, radiation use efficiency (Kiniry et al., 2005). The fraction of intercepted photosynthetically active radiation can be used to estimate the leaf area index (LAI) through its relationship with the plant canopy (Johnson et al., 2010).

This provides an easy and non-destructive way of estimating the leaf area index. IPAR can be accurately determined using a ceptometer, though care should be taken to avoid confounding factors such as the soil albedo, row spacing and lack of canopy uniformity (Andrade et al., 2002).

Quantitative understanding of the ability of cassava landraces to convert intercepted (PAR) into dry matter is important in enhancing adaptive strategies to improve cassava yield.

### **2.13 Summary**

Most studies in the literature have quantified the difference in gaseous exchange and root yield of cassava genotypes (Ogola and Mathews, 2011; El-Sharkawy, 2016, De Souza et al., 2016; Phoncharoen et al., 2019). There is significant literature on climatic, soil, nutrient, rainfall, soil moisture, biomass, root yield, evapotranspiration, soil water use efficiency by cassava (*Manihot esculenta Crantz*) Okogbenin et al., 2003; Siahpoosh and Dehghanian, 2012; Polthanee and Srisutham, 2018). However, limited studies have been done in subtropical ecological regions to investigate variation in water use efficiency, gaseous exchange and yield of cassava landraces. Therefore, such studies are important as they provide data on the behaviour of photosynthesis on water use and water use efficiency. It is also necessary for designing management strategies to enhance productivity and yield of cassava grown under low and erratic rainfall conditions of South Africa.



### CHAPTER 3. EVALUATION OF ROOT YIELD AND BIOMASS PRODUCTION AMONG FOUR CASSAVA LANDRACES GROWN IN THE DRY ENVIRONMENT OF LIMPOPO, SOUTH AFRICA.

#### ABSTRACT

Cassava (*Manihot esculenta* Crantz) is a root crop of importance in tropical and subtropical regions where periodic dry seasons and rainfall affect yield. This study determined the difference in root yield and yield components of four cassava landraces grown in the north-eastern part of South Africa. Two field trials were conducted during 2016/2017 (wetter) and 2017/2018 (drier) cropping season at the University of Venda's experimental farm. The trials were laid in a Randomized Complete Block Design consisting of four cassava landraces (ACC#1, ACC#2, ACC#3, and ACC#4) replicated three times. Mature cassava stem cuttings of 30 cm long, were planted manually at a spacing of 1 m x 1 m in both seasons. Each experimental unit consisted of six plant rows of 6 m length (36 m<sup>2</sup>) and 8 rows of 8 m length (64 m<sup>2</sup>) in 2016/17 and 2017/2018 cropping season, respectively. Root yield and yield components were determined at 311 days after planting (DAP) in both seasons. Root yield and total biomass varied with landraces from 9.5 t ha<sup>-1</sup> (ACC#4) to 11.9 t ha<sup>-1</sup> (ACC#3) and 18.2 t ha<sup>-1</sup> (ACC#4) to 22.0 t ha<sup>-1</sup> (ACC#1), respectively in the wetter season (2016/2017) but landraces did not affect root yield and aboveground biomass was observed in the drier (2017/2018) cropping season. The variation in root yield in the wetter season was associated with a similar variation in root girth and the number of roots per plant. There was a significant positive correlation between root yield and aboveground biomass (0.205\*), root girth (0.489\*), weight per root (0.528\*\*), root length (0.750\*\*\* and harvest index (0.714\*\*\*). Although the genotype x cropping season interaction did not affect root yield and yield components, root yield and yield components were greater in the wetter compared to the drier season as expected. These preliminary results suggest that ACC#3 and ACC#1 may be more adapted to this region than the other two landraces. However, there is a need for further evaluation of the landraces under different moisture regimes, within the same season, before any definite conclusions on their suitability in cassava improvement programmes can be drawn.

**Keywords:** Aboveground biomass, cassava, harvest index and root yield.

### 3.1 INTRODUCTION

Cassava (*Manihot esculenta Crantz*) is an important food crop and source of calories for more than 900 million people in the tropical and subtropical regions of Africa, Asia, and Latin America (FAO, 2018; Kouassi et al., 2018). It plays an important role in terms of food security, employment and income generation for farm families in developing tropical countries (De Souza et al., 2016; FAO, 2018). The crop is grown by most smallholder farmers due to its greater water use efficiency and the ability to yield better than other staple food crops under water limiting conditions and poor soils (El Sharkawy, 2006; Ceballos et al., 2011; Esuma et al., 2016; Phoncharoen et al., 2019). Indeed, cassava can be cultivated in areas receiving less than 300 mm rainfall per year with a dry season of four to six months (El-Sharkawy, 1993); under prolonged water shortages in seasonally dry and semiarid environments with less than 700 mm of annual rain, improved cultivars can give dry root yields of over 3 t ha<sup>-1</sup> (El-Sharkawy, 2006). However, although cassava can grow on marginal areas where cereals and other crops do not grow well (due to its tolerance to drought and low-nutrient soil), with better planting material and improved input management, the productivity of cassava could be doubled (Zhang et al., 2000) since cassava requires optimal conditions to achieve high growth rates.

Total world cassava production is expected to increase from 172.7 million to 273 million tons in the period 1993-2020 with Nigeria being the world's largest producer (Kouassi et al., 2018; FAO, 2018) but a higher projection of demand and production growth estimates the 2020 production at 291 million tons (Scott et al., 2000; Kouassi et al., 2018). On a global basis, cassava is ranked as the sixth most important source of calories in the human diet after rice, maize, wheat, soybean and potato (Okogbenin et al., 2013; FAO, 2018) but in sub-Saharan Africa, it is the third-largest source of carbohydrates (Abdoulaye et al., 2012, Utomo et al., 2017). About 70% of world cassava root production is used for human consumption either directly after cooking or in processed forms; the remaining 30% is used as an important industrial raw material for the production of starch, alcohol, pharmaceuticals, gums, confectioneries, biofuel, and livestock feed (Chetty et al., 2013; Zhang et al., 2014). In many parts of Africa, the leaves and tender shoots are also consumed as vegetables (Latif and Müller, 2015).

Cassava root yields vary greatly largely due to variation in climate, soil, genotypes as well as management practices. For example, root yield of cassava range between 31.2 t ha<sup>-1</sup> and 56.2 t ha<sup>-1</sup> in the dry and semi-arid Colombia (El-Sharkawy, 2007), 12.1 t ha<sup>-1</sup> and 25.7 t ha<sup>-1</sup> under irrigation in Brazil (El-Sharkawy, 2006), 9.8 t ha<sup>-1</sup> and 48.6 t ha<sup>-1</sup> in East Java, Indonesia (Utomo et al., 2017), 11.4 t ha<sup>-1</sup> and 19.7 t ha<sup>-1</sup> under rain-fed conditions in Eastern Uganda (Mulualem and Ayenew, 2012), 7.7 t ha<sup>-1</sup> and 20.8 t ha<sup>-1</sup> in Côte d'Ivoire (Kouassi et al., 2018) and 14.24 t ha

<sup>1</sup> and 34.09 t ha<sup>-1</sup> averaged across different environments in Nigeria (Fisher and Edmeades, 2010). Preliminary studies in northeastern South Africa recorded huge cassava root yield, 38.4 to 52.7 t ha<sup>-1</sup>, without irrigation and fertilizer additions (Ogola and Matthew, 2011) suggesting that cassava may be well adapted to this environment.

It is clear from the foregoing that there is a huge variation in cassava root yields across and within regions which is perhaps attributed to differences in climate, soils, genotypes and management practices but drought appears to be the major cause of low yield due to its effects on plant growth and development (El-Sharkawy and De Tafur, 2010; Rosenthal et al., 2012). Therefore, root yields of cassava may be improved through continuous cassava improvement programmes, judicious selection of genotypes as well as manipulation of management practices.

The hypothesis tested in this study was that there is genotypic variation in root yield and yield components among four cassava landraces collected from one region of northeastern part of South Africa. Therefore, the study assessed the differences in root yield and yield components of four cassava landraces grown under rain-fed conditions at Thohoyandou, a representative location of the dry environments of northeastern South Africa.

## 3.2 MATERIALS AND METHODS

### 3.2.1 Experimental design and management

Two trials were conducted over two successive seasons at the University of Venda's experimental farm, which is situated at Thohoyandou (22° 58.081'S, 30° 26,411'E, and 595 m asl), Limpopo Province, South Africa. The site is characterized by an annual rainfall of around 500 mm that falls mainly in summer, and average maximum and minimum temperature of 31 °C and 18 °C, respectively (Tadross et al., 2006). The soils at the site are predominantly deep, well-drained clays with slightly acidic pH (Soil classification working group, 1991).

The experiments were laid out in a Randomized Complete Block Design (RCBD) consisting of four cassava landraces (ACC#1, ACC#2, ACC#3 and ACC #4) replicated three times. Mature cassava stem cuttings of 30 cm long, were planted manually at a spacing of 1 m x 1 m in 2016/2017 and 2017/2018 cropping season. Each experimental unit consisted of six plant rows of 6 m length (36 m<sup>2</sup>) and 8 rows of 8 m length (64 m<sup>2</sup>) in 2017/2018 cropping season. The experiments were under rain-fed conditions without fertilizer additions and the plots were kept weed-free throughout the experimental period.

### 3.3 Data collection and statistical analysis

Twenty-four (2016/2017) and thirty-six (2017/2018) cassava plants, from the 4 and 6 innermost rows respectively, from each experimental plot were harvested at 10 months after planting (MAP) for determination of root yield and yield components. The harvested roots were chopped into small pieces (about 1cm thick) and oven-dried at 70 °C until a constant weight was achieved. The proportion of dry matter content was calculated as shown in equation 1.

$$\text{Dry matter (\%)} = \frac{\text{Dry weight}}{\text{Fresh weight}} \times 100 \quad 1$$

Ten roots (per plot) were sub-sampled from all the harvested plants and used for the determination of root length (cm), root girth (cm), number of storage roots and mean root weight (g plant<sup>-1</sup>). Root yield and aboveground biomass were determined from all the harvested plants in both seasons. Root length was measured from one tip to the other using a measuring tape; root girth was determined from the same roots using Vernier callipers by measuring the apical and distal ends as well as the middle of each root and taking the average; number of storage roots per plant was determined by counting; mean root weight (g plant<sup>-1</sup>) was determined from the weight of the roots from the ten sub-sampled plants from each plot. Root yield and

aboveground biomass were determined from all the harvested plants in both seasons. Harvest index was determined as the ratio of root yield to total above-ground biomass.

All data were subjected to one-way analyses of variance (ANOVA) using GenStat 18<sup>th</sup> Edition. Means were separated using the standard error of difference (S.E.D) when F-test indicated significant differences among the treatments. Correlation analysis was conducted to assess the relationships between root yield and yield components.

## 3.4 RESULTS

### 3.4.1 Weather data

Nine rainfall events were observed during 2016/2017 cropping season (Table 3.1), giving a total of 1411.2 mm of rainfall however, there was no rainfall in June and July. December and January had the highest amount of rainfall (416.3 mm) and (402.8 mm), respectively. A total of 1205.2 mm of rain occurred during crop establishment period (December to March) while bulking period (May to August) had a total of 206.0 mm of rainfall. In contrast, eleven rainfall events were observed during 2017/2018 (Table 3.1), March to April had the highest amount of rainfall (388.6 mm, 109.2 mm and 133.5 mm), respectively. A total of 672.4 mm of rain occurred during crop establishment (February to May) while during bulking period (May to August) had a total of 68.1 mm of rainfall (Table 3.1). Although, mean temperatures recorded were the same in both seasons, a higher temperature of 19.2 °C was recorded in the drier season during bulking (April to October) compared to air temperatures observed during crop establishment (January to March). The average maximum and minimum air temperatures were 30.50 and 15.35 °C for 2016/2017. Similarly, maximum and minimum air temperatures were 28.37 and 15.01 °C for 2017/2018 cropping season. Rainfall distribution during 2016/2017 was better compared to 2017/2018. Cassava is highly sensitive to soil water deficit during the first three (3) months of planting (Agili and Pardales, 1997). Hence, low rainfall during crop establishment in 2017/2018 cropping season might have reduced the growth and productivity of the crop significantly, particularly the growth of roots and shoots which subsequently affected the storage roots during bulking.

### 3.4.2 Root yield and yield components

There was no variation in root yield and yield components amongst the landraces in 2017/2018 cropping season but genotypes affected aboveground biomass, root girth, number of roots per plant and root yield in 2016/2017 cropping season (Table 3.2). Number of roots (per plant) was 81% and 62% greater in ACC#3 and ACC#2 (6.7 & 6.0, respectively) compared with ACC#1 and ACC#4, which both recorded 4 roots per plant (Table 3.2). Similarly, root girth was greater in ACC#3 (17.8 cm) and ACC#2 (18.2 cm) compared to ACC#1 (14.1 cm) and ACC#4 (12.9 cm), which were statistically the same (Table 3.2). In contrast, total biomass and root yield were greater in ACC#3 (20.7 and 11.9 t ha<sup>-1</sup>, respectively) and ACC#1 (22.0 and 11.3 t ha<sup>-1</sup>, respectively) compared to ACC#2 and ACC#4 with root yields of 10.2 and 9.5 t ha<sup>-1</sup>, respectively (Table 3.2). Although the genotype x cropping season interaction did not affect root yield and yield components, root yield (by 33.8%; 2.7 t ha<sup>-1</sup>) and yield components were greater in the wetter compared to the drier season as expected (Table 3.4). There was a significant positive correlation

between root yield and aboveground biomass (0.847\*\*\*), root girth (0.489\*), weight per root (0.528\*\*), root length (0.750\*\*\*) and harvest index (0.714\*\*\*) (Table 3.5).



Table 3.1 Summary of weather data at Thohoyandou, during the 2016/2017 and 2017/2018 cropping season. Monthly totals or means values are given.

Year	DEC	JAN	FEB	MARCH	APRIL	MAY	JUNE	JULY	AUG	SEP	OCT	Total/Mean
2016/2017												
Solar radiation (MJ m <sup>-2</sup> d <sup>-1</sup> )	16.2	15.2	15.8	16.3	13.2	13.2	11.5	11.6	13.5	15.7	16.7	14.5
Mean RH (%)	69.8	77.8	77.4	71.9	74.7	68.1	65.5	62.2	58.8	57.4	64.1	68.0
Rainfall (mm)	416.3	402.8	275.6	110.5	77.5	17.5	0.0	0.0	14.5	44.5	52.1	1411.2
Mean Temp (°C)	24.8	24.0	24.2	23.5	21.3	19.3	17.8	18.1	18.7	21.3	23.2	21.5
2017/2018												
Solar radiation (MJ m <sup>-2</sup> d <sup>-1</sup> )	18.5	19.4	12.5	20.1	14.2	12.5	11.8	13.3	15.5	10.7	14.6	14.8
Mean RH (%)	64.3	59.1	78.8	68.0	66.7	62.2	58.2	57.8	55.9	54.4	57.5	62.1
Rainfall (mm)	0.8	1.3	388.6	109.2	133.5	41.1	2.0	31.0	27.4	3.5	2.8	740.5
Mean Temp (°C)	24.9	25.2	22.5	24.8	20.5	19.9	19.4	19.6	18.0	20.9	21.4	21.6



Table 3.2: Variation in yield and yield components of the landraces at harvest in 2016/2017 cropping season.

Genotype	Total biomass (tha <sup>-1</sup> )	Dry matter (%)	Root girth (cm)	Root no./plant (g plant <sup>-1</sup> )	Mean root yield (g plant <sup>-1</sup> )	Above-ground biomass (t ha <sup>-1</sup> )	Root yield (t ha <sup>-1</sup> )	Root length (cm)	Harvest Index (%)
ACC#1	22.00 <sup>c</sup>	30.80	14.1b <sup>c</sup>	3.70 <sup>a</sup>	13.40	10.70	11.30 <sup>ab</sup>	32.60	51.10
ACC#2	18.90 <sup>a</sup>	28.20	18.20 <sup>a</sup>	6.00 <sup>b</sup>	12.40	10.20	10.20 <sup>ab</sup>	29.40	54.00
ACC#3	20.70 <sup>ab</sup>	34.20	17.80 <sup>a</sup>	6.70 <sup>b</sup>	11.40	11.90	11.90 <sup>c</sup>	34.70	57.20
ACC#4	18.20 <sup>a</sup>	24.70	12.90 <sup>c</sup>	3.70 <sup>a</sup>	9.50	9.50	9.50 <sup>a</sup>	26.00	51.80
P-value	**	ns	*	**	ns	ns	*	ns	ns
CV (%)	4.2	18.0	12.1	13.5	15.3	15.3	16.6	16.6	24.9
S.E.D.	0.70	3.90	1.56	0.60	1.50	1.5	0.80	4.10	0.02

\*, \*\* = significant at P<0.05, at P<0.001 and ns = not significant (P>0.05), C. V= coefficient of variation



Table 3.3: Variation in yield and yield components of the landraces at harvest in 2017/2018 cropping season.

Genotype	Total biomass (tha <sup>-1</sup> )	Dry matter (%)	Root girth (cm)	Root no/plant (g plant <sup>-1</sup> )	Mean root yield (g plant <sup>-1</sup> )	Above-ground biomass (t ha <sup>-1</sup> )	Root yield (t ha <sup>-1</sup> )	Root length (cm)	Harvest Index (%)
ACC#1	14.90	25.50	46.70	5.42	29.70	9.20	8.24	35.10	56.90
ACC#2	17.10	28.60	44.50	8.26	28.60	6.60	7.94	29.30	45.80
ACC#3	21.90	36.20	42.40	7.61	30.20	13.50	8.4	27.10	39.30
ACC#4	15.90	21.90	33.60	6.71	26.30	8.60	7.32	27.20	49.50
F-ratio	ns	ns	ns	ns	ns	ns	ns	ns	ns
S.E.D.	3.560	0.078	5.910	2.344	3.780	0.269	0.75	0.262	0.319
CV (%)	24.9	19.4	17.3	11.4	16.1	14.1	16.1	16.8	12.2

\*, \*\* = significant at P<0.05, at P<0.001 and ns = not significant (P>0.05), C.V= coefficient of variation



Table 3.4: Interaction between root yield, yield components and seasons/year.

Season/Year	Dry matter (%)	Fresh root weight (g plant <sup>-1</sup> )	Aboveground biomass (t ha <sup>-1</sup> )	Mean root weight (g plant <sup>-1</sup> )	Root no /plant (g plant <sup>-1</sup> )	Root yield (t ha <sup>-1</sup> )	Root girth (cm)
2016/2017	34.10	93.10	0.60	11.80	5.00	10.70	15.80
2017/2018	28.00	74.10	2.00	28.70	7.00	8.00	41.80
Genotype							
ACC#1	27.70	83.70	1.20 <sup>a</sup>	21.60 <sup>a</sup>	4.50	9.80	30.40
ACC#2	32.20	80.10	1.30 <sup>a</sup>	20.50 <sup>b</sup>	7.10	9.10	31.40
ACC#3	34.90	85.80	1.60 <sup>b</sup>	21.10 <sup>a</sup>	7.10	10.10	30.10
ACC#4	29.50	84.50	1.20 <sup>b</sup>	17.90 <sup>c</sup>	5.20	7.40	23.30
F-ratio	ns	ns	ns	ns	ns	ns	ns
Genotype (G)	ns	ns	*	*	ns	ns	ns
Year (Y)	**	**	**	**	**	**	***
Y × G	ns	ns	ns	ns	ns	ns	ns
S.E.D.	2.20	3.61	0.09	1.34	0.57	0.55	2.18
CV (%)	17.4	15.0	17.4	18.2	13.3	14.4	18.5

\*, \*\*, \*\*\* = significant at P<0.05, P<0.01, P<0.0001 and ns = not significant (P>0.05), C.V= coefficient of variation.



Table 3.5: Correlations between root yield and yield components in 2016/2017 cropping season.

Root Yield (tha <sup>-1</sup> )	Root yield	Mean root weight	AGB	Total biomass	Root length
Mean root weight (g plant <sup>-1</sup> )	0.5287**				
Aboveground biomass (t ha <sup>-1</sup> )	0.2055*	-0.5738ns			
Total biomass (t ha <sup>-1</sup> )	0.8471***	0.5095**			
Root length (cm)	0.7505***	0.6019***	0.5685**		
Root girth (cm)	0.4899**	0.1543*	0.1670*	0.3946*	
Number of roots plant (g plant <sup>-1</sup> )	0.2525*	0.0003ns	-0.1259ns	0.2762*	0.7005***

### 3.5 DISCUSSION

Root yield varied with genotypes in the wetter (2016/2017) but not in the drier (2017/2018) cropping season. The variation in root yield in 2016/2017 was associated with a similar variation in number of roots per plant, mean root weight, aboveground biomass, root girth, root length and harvest index; this implies that high root length coupled with increased root size could have resulted in yield improvement in 2016/2017 cropping season as early observed by Aina et al. (2007). The variation in root yield amongst the landraces may, in part, be attributed to variability in the rate of storage root bulking (Okogbenin et al., 2003; Suja et al., 2006). Fast bulking genotypes begin storage root development and shoot simultaneously, which varies from those of late- or slow-bulking genotypes, which develop sufficient aboveground biomass before storage root bulking commences (Alves, 2002.). Early-maturing genotypes exhibit maximum bulking rates during their early growth stages compared with late-maturing genotypes (Baker et al., 1989). This pattern depends on the growth conditions, particularly moisture, which may affect the choice of sink and hence environmental conditions that curtail storage root bulking will adversely affect late-bulking genotypes compared with early-bulking genotypes due to their differential sink–source relationships at the different stages in their phenology (Ober and Sharp, 2007).

Cassava root yield was greater in 2016/2017 compared to 2017/2018 cropping season probably due to the higher rainfall in the former season. Similar results were found by Baker (1989) and Odubanjo et al. (2011). This may be due to poor crop establishment which was caused by the shortage of water from the first 2 to 8 weeks after planting. Studies also have shown that a single rainfall event that occurs the few days after planting may promote better crop establishment hence root yield (Martin et al., 2018).

This suggests that although cassava is known to be fairly drought-tolerant, soil moisture availability has a huge effect on its yield (El-Sharkawy, 1993; Shan et al., 2018). Indeed, a single rainfall event that occurs few days after planting, may promote better crop establishment and root yield (Martin et al., 2018) as observed in 2016/17 cropping season compared with 2017/18 cropping season where there was lower rainfall during the first two and half months after planting. Although there is no data on canopy cover in 2016/2017 cropping season, the canopy cover was low in 2017/2018 during bulking period (May to August) (Figure 5.1) which suggests poor establishment in that season.

Although the root yield was lower in the drier compared to the wetter season, the yields were still relatively high in the drier season which signifies the importance of cassava as an insurance and food crop in the dry environments. However, there was no significant interaction between genotypes and year which may suggest that the studied landraces did not differ in their response to variation in soil moisture availability.

There was a positive correlation between root yield and harvest index in 2016/2017 cropping season which suggests that the high yielding landraces (ACC#3 & ACC#1) were able to not only accumulate high crop biomass but to also partition most of the biomass into the storage roots (Lemoine et al., 2013; Phoncharoen et al., 2019). Harvest index, which indicates the accumulation of dry matter into the economic parts of the plant (Alves, 2002; El-Sharkawy, 2004) was also found to be positively correlated with root yield. However, the positive correlation between root yield and harvest index may be not an indication of high yield potential. For instance, a less vigorous, short cassava plant with a vigorous root system may have a high harvest index but not high root yield per se. For this reason, a yield standard should be set and landraces that exceed such a target with desirable harvest index should be selected (Aina et al., 2007; Adjebeng-Danquah et al., 2012). The current results of root yield and yield components (such as mean root weight, fresh shoot weight, and root girth) are comparable to previous findings across different environments (Okogbenin et al., 2002; Aina et al., 2009, 2010; Mutegi-Murori, 2009; Temegne et al., 2016). However, the root yields from the current study were much lower than previous ones from the same site as the current study (Ogola and Mathew, 2011) probably due to much higher rainfall received in the earlier study as well as the differences in the genotypes used.

It is clear from the foregoing that environmental and crop genotypes have huge influence on agronomic performance of cassava in this part of northeastern South Africa as well as in other parts of the world and therefore number of studies across sites and years are highly encouraged before any tangible recommendations on the suitability of a genotype either for release or to be used in crop improvement programmes can be made.

### **3.6 CONCLUSION**

This study assessed the variation in root yield and yield components among four cassava landraces grown over 2 seasons in Thohoyandou, Limpopo Province, South Africa. Root yield and its components varied with genotypes and the high yields were recorded in ACC#1 & ACC#3 in both seasons. Season 1 had greater root yield, harvest index, and total biomass compared to season 2. The results from this study determined that ACC#3 & ACC#1 produced significantly

higher storage root fresh weight per plant and subsequently high storage root yield in 2016/2017 than other genotypes. Therefore, we recommend further evaluation of the 2 landraces and its possibility of using the landraces in cassava improvement programmes.

## CHAPTER 4: VARIATION IN WATER USE AND WATER USE EFFICIENCY AMONG FOUR CASSAVA LANDRACES GROWN IN THE DRY ENVIRONMENT OF LIMPOPO, SOUTH AFRICA.

### ABSTRACT

Cassava is mainly grown on stored soil water in areas where it is cultivated. As such, the crop has to strike a balance in water use to ensure that there is enough soil moisture towards the end of the growing season and at the same time to have extracted enough water to sustain yield. The pattern of water extraction could be mitigating by adopting cassava landrace with higher (WUE). Therefore, improving cassava production in water limiting conditions requires the use of cassava varieties which are efficient in the use of limited soil moisture to maximize yield. This study evaluated variation in the water use and water use efficiency of four cassava landraces grown in the north-eastern part of South Africa. Two field experiments were conducted during the 2016/2017 and 2017/2018 cropping season at the University of Venda's experimental farm. The trials were laid in a Randomized Complete Block Design consisting of four cassava landraces (ACC#1, ACC#2, ACC#3, and ACC#4) replicated three times. Mature cassava stem cuttings of 30 cm long, were planted manually at a spacing of 1 m x 1 m in both seasons. Each experimental unit consisted of six plant rows of 6 m length (36 m<sup>2</sup>) and 8 rows of 8 m length (64 m<sup>2</sup>) in the 2016/17 and 2017/2018 cropping season, respectively. Soil moisture content was measured at seven days' interval from sowing until harvest using a neutron probe and the data used to determine water use (WU), Water-use efficiency for root yield (WUE<sub>rt</sub>) and water use of biomass production (WUE<sub>b</sub>). (WUE<sub>rt</sub>) and (WUE<sub>b</sub>) varied with landraces in season I from 37.0 kg ha<sup>-1</sup> mm<sup>-1</sup> (ACC#4) to 46.60 kg ha<sup>-1</sup> mm<sup>-1</sup> (ACC#3) and between 71.30 kg ha<sup>-1</sup> mm<sup>-1</sup> (ACC#2) to 86.0 kg ha<sup>-1</sup> mm<sup>-1</sup> (ACC#1) respectively. Genotypes did not differ in their water use and soil moisture extraction patterns. There was a significant positive correlation between yield WUE<sub>rt</sub> (0.963<sup>\*\*\*</sup>) and production WUE<sub>b</sub> (0.847<sup>\*\*\*</sup>). The results of this study indicated that ACC#3 and ACC#1 were able to use water more efficiently in 2016/2017 and thus outperformed the other two landraces but did not appear to have any water use and yield advantage in the drier cropping season. However, there is a need for further evaluation of the landraces under different moisture regimes.

**Keywords:** Cassava, crop water use, evapotranspiration, landraces, soil water depletion.



## 4.1 INTRODUCTION

Cassava (*Manihot esculenta Crantz*) has the ability to grow in marginal ecologies where other crops fail (Okogbenin et al., 2003; El-Sharkawy, 2007). Several studies have attributed cassava's ability to grow in these ecologies to its hardiness and ability to tolerate dry conditions through enhanced water use efficiency (El-Sharkawy and Cock 1984; Okogbenin et al., 2003; El-Sharkawy, 2004). Effective identification of physiological traits associated with water use efficiency in cassava has been very difficult (El-Sharkawy, 2007). Various physiological and morphological mechanisms are used by cassava for survival under dry environments and erratic rainfall which can be exploited (El-Sharkawy, 2007). Cassava plays a central role in food and economic security for small-holder farmers and holds an unrealized potential as a cash and food crop as it is widely grown and is well-adapted into the farming systems. Generally, cassava serves five purposes: famine reserve crop, a rural food staple, a cash crop for urban consumption, industrial raw material, and foreign exchange earner (Nweke et al., 2004). The crop is renowned for its drought tolerance and hardiness in stressful environments (El-Sharkawy, 2004). This drought tolerance mechanism leads to high crop water use efficiency and positions the crop as a more efficient crop, which can take advantage of global climate change, than other food crops.

Cassava is grown by most smallholder farmers due to its greater water use efficiency (WUE) as well as, ability to yield better than other staple food crops under conditions of extended drought and poor soils (Esuma et al., 2016, Ceballos et al., 2011; El-Sharkawy, 2007). Optimum root yields of cassava are often affected by the availability of water stored in the soil profile, the pattern of water extraction and the efficiency in which the extracted water is used (Al-Kaisi and Broner, 2009). As the water dries up in the soil profile, it becomes challenging for the plant to extract the available stored water. Similarly, WUE is affected by dry matter accumulation, evapotranspiration, and photosynthesis (Olanrewaju et al., 2009; Polthanee and Srisutham, 2018). Studies show that low water use and water use efficiency (WUE) may result in low yield in cassava (Okogbenin et al. 2003) and other crops (Monneveux et al., 2013). However, genotypes with greater water use efficiency have been reported to decrease leaf water loss, which can reduce damage to plants and enable them to maintain higher net photosynthetic rate, which plays an important role in improving WUE and yield of cassava (Siahpoosh and Dehghanian, 2012; Polthanee and Srisutham, 2018). Indeed, the pattern of moisture extraction of cassava depends on the soil moisture supply and the yield level and there is usually a close linear relationship between the amount of water used and root yield (Mahakosee et al., 2019).

Water use efficiency has various definitions depending on the level and measurement scale, but for this chapter, it will be defined as the ratio of root yield to water used (Condon et al., 2004). There have been reports that there is genetic variation in WUE in various crops including cassava (Siahpoosh and Dehghanian, 2012; Polthanee and Srisutham, 2018). For example, WUE of cassava genotypes ranged between 27.4 kg ha<sup>-1</sup> mm<sup>-1</sup> and 35.3 kg ha<sup>-1</sup> mm<sup>-1</sup> for cassava grown in the late rainy season of Northeastern Thailand (Polthanee and Srisutham, 2018), 18.6 kg ha<sup>-1</sup> mm<sup>-1</sup> and 34.4 kg ha<sup>-1</sup> mm<sup>-1</sup> in the dry-lands of Eastern Uganda (Mulebek et al., 2015), whereas Odubanjo et al. (2011) reported WUE values of between 15.6 and 20.0 kg ha<sup>-1</sup> mm<sup>-1</sup>, Olanrewaju et al. (2009) also reported WUE values of between 19.2 kg ha<sup>-1</sup> mm<sup>-1</sup> and 23.3 kg ha<sup>-1</sup> mm<sup>-1</sup> in Nigeria. It is clear that there is a huge variation in WUE which may be attributed to variation of rainfall received or water supply, sites and genotype used. This may allow plant breeders to exploit this trait in improving crop yields under water limiting conditions, especially under stored soil water. Improvement of WUE requires a multifaceted strategy (Wang et al., 2002) which includes breeding and management practice such as genotype selection (Condon et al., 2004). Some of the management practices that increase WUE include using genotypes with a greater pattern of water extraction since it ensures maximum use of available soil water (Merrill et al., 2007).

Furthermore, although water use efficiency has been studied extensively in cassava, there are very few reports in the literature that have comprehensively described the variation in the actual pattern of water extraction, and water use efficiency amongst cassava landraces in the high latitude semi-arid tropics where cassava growth and development is limited during winter months. Despite the evaluation of WUE in cassava in various studies, little has been achieved since these studies were focused on single factors affecting WUE. This may cause the variability of data from different studies due to the failure of the integration of various factors (Gan et al., 2010). The hypothesis tested in this study was that there is variation in the pattern of water extraction, water use and water use efficiency among four cassava landraces collected from northeastern part of South Africa. Therefore, the study assessed the variation in the pattern of water extraction, water use, and water use efficiency of four cassava landraces in Thohoyandou, a representative location of the dry environments of northeastern part of South Africa.

## 4.2 MATERIALS AND METHODS

Each chapter has more specific materials and methods including formulas. The study site, experimental design, treatments that were evaluated and agronomic practices are described in detail in Chapter 3.

### 4.2 Data collection

#### 4.2.1 Soil moisture

Soil moisture content was measured weekly, where possible, using a neutron probe (Hydroprobe, Model 503DR, 94553, USA) in both seasons. On each measurement occasion, the probe's radioactive source was lowered into access tubes that were installed immediately after planting, one between and within the plot, at a depth of 1.2 m and 64 second counts readings were taken at 30, 60, 90 and 120 cm depths. Before each day of measurement, standard counts were taken and used to calculate count ratios (count readings/standard count). Volumetric water content ( $Q_v$ ) at each depth was calculated using the calibration equation that is already developed for the site (Thangwana and Ogola, 2016) as shown below:

$$0.30 \text{ m depth: } V_{\theta} = 0.0818 x + 0.0268 \quad (1)$$

$$0.60 \text{ m depth: } V_{\theta} = 0.3227 x - 0.2733 \quad (2)$$

$$0.90 \text{ m depth: } V_{\theta} = 0.3736 x - 0.3297 \quad (3)$$

120 cm depth was calculated from equation 3 because there is no difference in soil properties and soil moisture between 90 cm and 120 cm depth.

Where  $x$  is the count ratio.

#### 4.2.2 The pattern of water extraction

Where,  $\theta$  is the volumetric water content in millimetres and  $C$  is the neutron counts. The soil water balance method (Equation 4) was used to estimate water use which was estimated to be equivalent to evapotranspiration from planting to physiological maturity as documented by Anwar et al. (1999).

### 4.2.3 Water use and water use efficiency

Crop water use (WU) was determined using the standard water balance equation:

$$WU = \Delta S + P + I + U - D - R = \Delta S + P + I + U - D - R \quad (4)$$

Where  $\Delta S$  is the change in storage (difference in volumetric water content of the entire profile between the first and last neutron probe readings), P is precipitation (mm), I is irrigation (mm), U is upward capillary, D is drainage and R is the surface runoff (Allen et al., 1998; Anwar et al., 1999). Considering the flatness of the field (less than 2% slope) and following earlier studies from the same site (Ogola and Thangwana, 2013; Ogola, et al., 2013; Lusiba et al., 2017), rate of infiltration, drainage, capillary rise, and surface runoff were assumed to be negligible. Therefore, WU was estimated as a function of change in storage and rainfall. Water use efficiency of root yield ( $WUE_{r}$ ) and water use efficiency of biomass production ( $WUE_{b}$ ) were determined using equations 5 and 6 below (Sinclair et al., 1984; Araus et al., 2002). Total biomass and root yield were determined from an area of 4 and 6 innermost rows respectively from each plot in the season I and II (See chapter 3).

$$WUE_{root\ yield} = \frac{Root\ Yield}{WU} \quad (5)$$

$$WUE_{biomass} = \frac{Total\ biomass}{WU} \quad (6)$$

All data were subjected to one-way analyses of variance (ANOVA) using GenStat 18<sup>th</sup> Edition based on Randomized Complete Block Design. Means were separated using the standard error of difference (S.E.D) when F-test indicated significant differences among the treatments. Correlation analysis was conducted to assess the relationships between the different parameters measured.

## 4.3 RESULTS

**Detailed weather data is presented in chapter 3:**

### 4.3.1 Soil water extraction

There was no significant variation in the pattern of soil water extraction among the landraces in both seasons. (Fig 4.1). In 2016/2017 landraces had greater water extraction compared to 2017/2018 in the soil layer (0-30cm), whilst in soil layer 30-60cm, it was 2017/2018 with greater soil water extraction compared to the 2016/2018 (Fig 4.1 and 4.2). Although between 35 DAP and 56 DAP there was a recharge of moisture due to rainfall, landraces started to extract more water between 56 DAP and 77 DAP in 2016/2017. Between 77 DAP and 105 DAP there was also recharge in moisture and landraces extracted greater amount of water between 105 DAP and 297 DAP with similar pattern whilst between 297 and 311 there was a recharge of water due to rainfall received.

In contrast, landraces did not affect water extraction in the soil layers (60-90 cm) and (90-120 cm) in 2017/2018. Between 35 DAP and 63 DAP in 2016/2017 and between 35 DAP and 77 DAP in 2017/2018 there was a recharge in water due to rainfall received at 60 cm soil depth. However, greater moisture extraction among all the landraces was observed between 56 DAP and 119 DAP in 2016/2017 and between 70 DAP and 276 DAP in 2017/2018. At 90 cm depth, greater moisture extraction was observed between 63 DAP and 311 DAP and a similar pattern of results was noted in both season I and II (Fig 4.1). In both seasons, a similar amount of water in all the soil layers was observed. Also, in the soil layer, 90-120 cm landraces did not affect soil water extraction patterns in 2017/2018. The same pattern of water extraction was observed in 2017/2018 while in 2016/2017 soil moisture content at 120 cm was not measured (Fig 4.1 and 4.2). Soil water measurements at the start of the experiments showed that soil water content ranged from 253.7 mm for ACC#2 to 255.7 mm for ACC#1 in 2016/2017, and 73.7 for ACC#4 to 79.2 for ACC#3 mm in 2017/2018 cropping season. In general, more water was used in 2016/2017 than the 2017/2018 cropping season (Table 4.1). The soil moisture change at 30-90 cm in the 2016/2017 and 2017/2018 cropping season was chosen to represent the soil moisture dynamics in the root-zone.

Although, there was considerable variation in water storage in the soil profile probably due to the difference in soil content and soil depths, change in soil water storage showed a similar pattern. During winter, when leaf areas and evaporative demand was small, rainfall exceeded evapotranspiration and water were stored in the soil profile in 2017/2018 (Figure 4.2). The soil

had the highest amount of water storage from December to March in 2016/2017 and February to April in the 2017/2018 cropping season, rainfall was also experienced in 2017/2018 during winter (see Table 3.1). Evapotranspiration (ET) increased as evaporative demand and leaf area increase from March to May when an ideal combination of temperature and moisture availability during vegetative crop growth (Figure 4.2). Total ET was regulated by seasonal rainfall and it was higher in the wetter than in the drier season. Plants accessed moisture in the topsoil layer (up to 30 cm) in the early growing stage and reached a peak extraction around the vegetative stage. In both 2016/2017 and 2017/2018 cropping season, plants had deeper roots which extracted soil moisture from as far as 60 cm below the soil surface (Figure 4.1). There was a sharp decline in soil water from the vegetative stage onwards in both 2016/2017 and 2017/2018 cropping season (Figures 4.1 and 4.2).

#### **4.3.2 Water use**

Soil water measurements at the start of the experiment showed that soil volumetric water content ranged from 253.7-255.7 mm in 2016/2017, and 73.7 -279.2 mm in 2017/2018. Although, there was no significant variation among the landraces higher average water use by the landraces in ACC#3 in both seasons (Figure 4.1). In 2016/2017 lowest crop water use was recorded in ACC#2 whist in 2017/2018 cropping the lowest crop was use was observed in ACC#4. All the landraces had greater water use in season 1 compared to season 2, due to the variation in rainfall received in both seasons (Figure 4.2). The plants used water from the top 30 cm during the vegetative phase and later accessed soil moisture deeper in the horizon.

#### **4.3.3 Water use efficiency of root yield and biomass production**

There was no variation in water use efficiency of root yield and biomass production amongst the landraces but in 2016/2017 landraces affected in water use efficiency of root yield and biomass production (Table 5.1). Water use efficiency of root yield varied ( $P \leq 0.05$ ) with landraces from ( $37.0 \text{ kg ha}^{-1} \text{ mm}^{-1}$  for ACC#4) to ( $46.60 \text{ kg ha}^{-1} \text{ mm}^{-1}$  for ACC#3) while water use efficiency of biomass production varied ( $P \leq 0.05$ ) from  $71.30 \text{ kg ha}^{-1} \text{ mm}^{-1}$  to  $86.0 \text{ kg ha}^{-1} \text{ mm}^{-1}$  in ACC#2 and ACC#1, respectively (Table 4.1). In the drier year, water use efficiency of root yield was considerably higher because of low rainfall received (Figure 4.1) and very lower water use by the landraces (Table 4.1).

#### **4.3.4 Water use, water use efficiency and yield relationships.**

There was a moderate positive correlation between water use and root yield (Table 4.2) Water use efficiency of root yield and biomass production was highly and positively associated with yield in 2016/2017 cropping season but no correlation was observed in 2017/2019 cropping season. Genotypes with high water use efficiency had the lowest yield while those with low water use efficiency had the highest yields.

Table 4.1. Genotypic and seasonal variation in water use and water use efficiency (of root yield and biomass production) in 2016/2017 and 2017/2018 cropping season under rain-fed conditions

Seasons	Water Use (mm)	WUE <sub>rt</sub> (kg ha <sup>-1</sup> mm <sup>-1</sup> )	WUE <sub>b</sub> (kg ha <sup>-1</sup> mm <sup>-1</sup> )
<b>2016/2017</b>			
ACC#1	255.7	46.3 <sup>b</sup>	86.00 <sup>b</sup>
ACC#2	253.7	40.3 <sup>b</sup>	74.58 <sup>ab</sup>
ACC#3	255.3	46.6 <sup>b</sup>	81.32 <sup>ab</sup>
ACC#4	255.4	37.00 <sup>a</sup>	71.35 <sup>a</sup>
F-ratio	ns	*	**
S.E.D	5.25	8.02	2.98
CV (%)	2.5	8.60	4.7
<b>2017/2018</b>			
ACC#1	74.5	15.3	204
ACC#2	76.8	27.5	228
ACC#3	79.2	27.1	240
ACC#4	73.7	19.0	218
F-ratio	ns	ns	ns
S.E.D	6.53	11.4	51.8
CV (%)	10.5	16.8	19.3
<b>Season/Year</b>			
2016/2017	255.9a	42.6	78.3
2017/2018	76b	22.2	222.4
F-ratio	ns	ns	ns
S.E.D	179.9	20.4	144.4
CV (%)	4.5	5.7	14.4
Year	***	***	***
Year ×	ns	ns	ns
<b>Genotypes</b>			

\*=P<0.05, \*\* = P<0.01, \*\*\*=P<0.001, and ns = not significant. C.V= coefficient of variation





Table 4.2. Correlations between root yield and WU,  $WUE_b$  and  $WUE_r$  in 2016/2017 and 2017/2018 cropping season.

Treatment relationship	Root yield * Water use	Root yield * $WUE$ of root yield	Root yield * $WUE$ of biomass production
2016/2017	0.2124*	0.986427***	0.8127***

\* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . Root yield, water use, water use efficiency of root yield, water use efficiency of biomass production and year

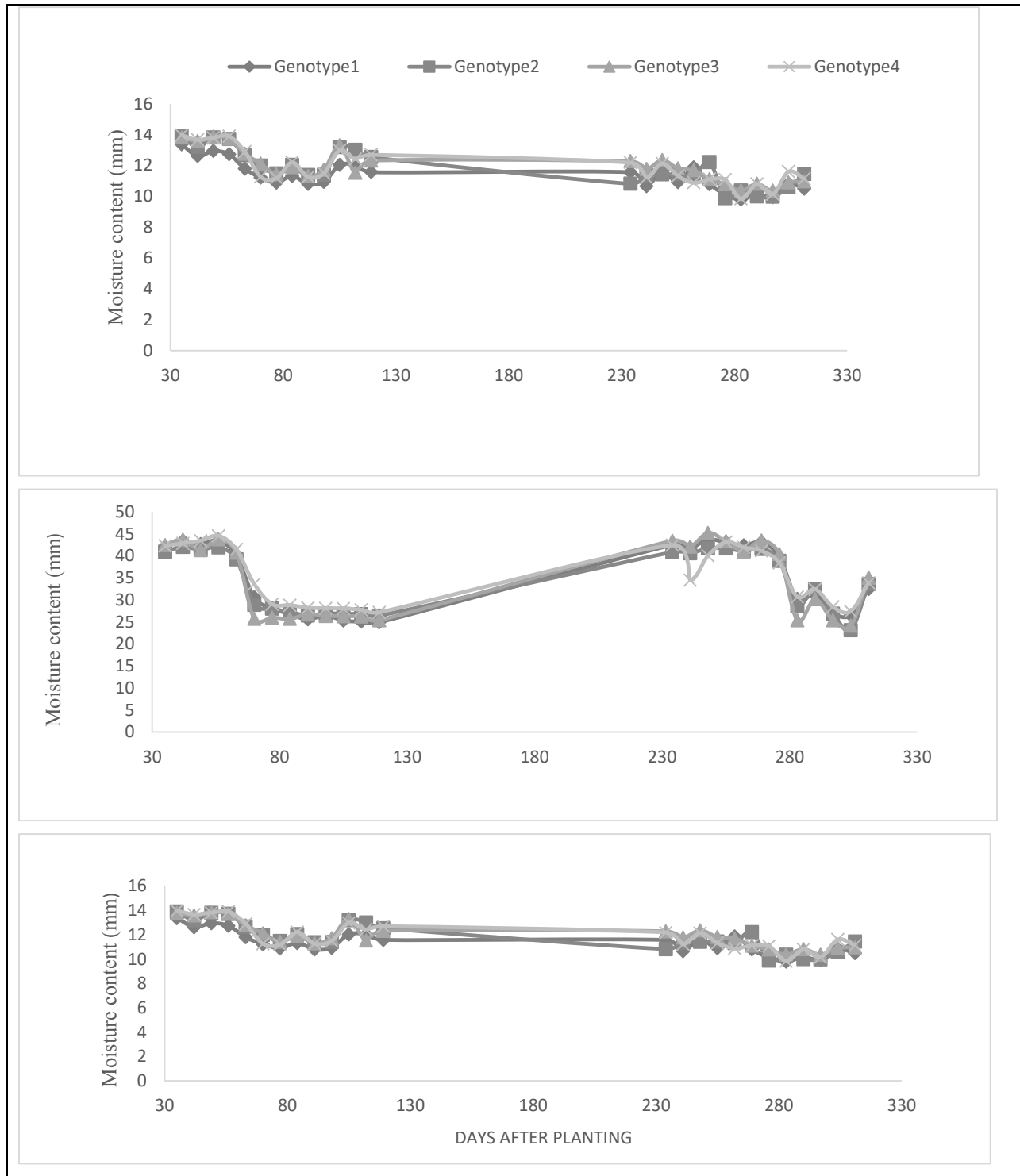


Figure 4.1: Variation in soil moisture content at 30 cm depth (a), 60 cm (60) and 90 cm depth (c) in 2016/2017 cropping season.

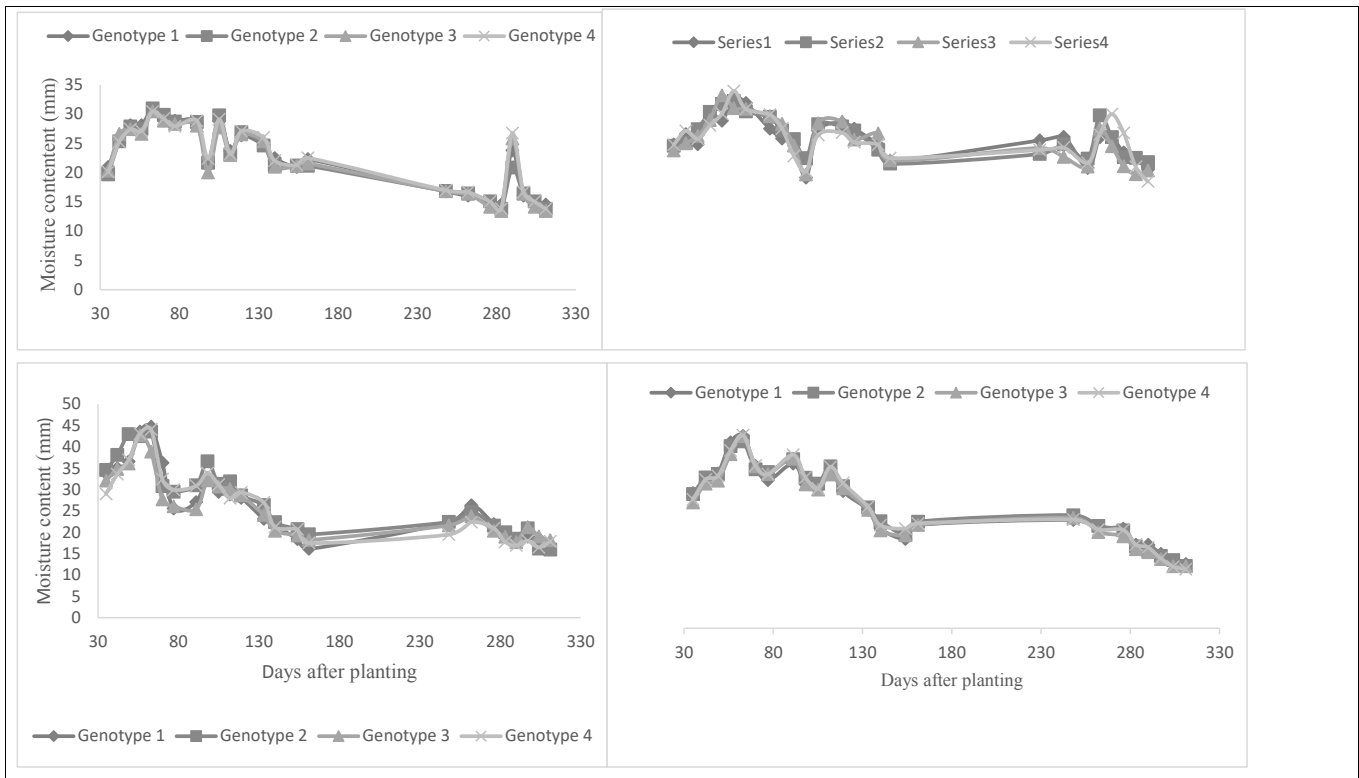


Figure 4.2: Variation in soil moisture content at 30 cm depth (a), 60 cm depth (b), 90 depth (c) and 120 cm depth in 2017/2018 cropping season.

## 4.4 Discussion

### 4.4.1 Soil moisture extraction and water use

Water use was not significantly different among the cassava landraces in both the wetter and drier seasons. Water use increased with rainfall and the main determinant of cassava root yield under rain-fed condition was rainfall during the growing season and its distribution. Cassava water use was higher in 2016/2017 compared to 2017/2018 cropping season (Table 4.1). This may be due to higher moisture availability in 2016/2017 cropping season compared to 2017/2018 cropping season (Figure 4.2) since water use in cassava depends on the levels of soil water available as observed by Bhardwaj (2001) and Odubanjo et al. (2011) in experiments conducted in the humid tropical environment of Nigeria. The higher soil water levels in 2016/2017 was highly due to the higher rainfall received in this season compared to 2017/2018 cropping season.

The greater moisture extraction may be attributed to the higher moisture levels in the wetter season compared to the drier season in 0-30 cm soil depth possibly caused by a high evaporation rate as observed by Bhardwaj (2001). Furthermore, the greater water extraction in 2016/2017 compared 2017/2018 cropping season in the soil layer (0-30 cm) during growing stage may have been caused by early canopy growth which demanded more water for growth.

Landraces did not affect water use in both seasons (Table 4.1). In the drier season, greater moisture extraction was observed in ACC#1 and ACC#3. However, cassava water use was generally higher under wetter compared to the drier season resulting from the rainfall received in season I. The water use values obtained in this current study ranged between 253.7 mm to 255.7 mm on average in 2016/2017 cropping season. In contrast, in 2017/2018 cropping season, water use ranged between 73.7 mm to 79.2 mm which was much lower than what other researchers has found (Table 4.1). However, Odubanjo et al (2011) reported the total water use of 651.13 mm for rain-fed experiment with a total rainfall of 872 mm and Olanrewaju et al (2009) reported WU values of between 430.0 and 1140.24 mm, respectively. The difference in water use values reported by different researchers may be due to different soil types, climate, and soil moisture availability levels and genotypes used. However, the difference in water use in the current study may the attributed to material used, management and prevailing climate.

#### 4.4.2 Water use efficiency of yield and WUE of biomass production

WUE of root yield was higher in 2016/2017 than in 2017/2018. The higher WUE of root yield in 2016/2017 may have resulted from root yield recorded due to rainfall distribution with higher rainfall in 2016/2017 than 2017/2018 cropping season. The values of water use efficiency of root yield in the current study are comparable to the findings by Polthanee and Srisutham (2018) who reported WUE of between 27.4 and 45.5 kg ha<sup>-1</sup> mm<sup>-1</sup> in the late rainy season of North-eastern Thailand. More even rainfall distribution leads to better utilisation of soil moisture and consequently, higher root yield which was observed in 2016/2017 cropping season. This was contrary to reports by Odubanjo et al. (2011) and Polthanee and Srisutham, (2018) who found that WUE was higher in rain-fed conditions compared to irrigated conditions.

Studies have reported that cassava, once it is established, can survive for several months without rain (El-Sharkawy, and Cock, 1984). Cassava adapts to drought by deep rooting and partial closure stomata (De Souza et al., 2016). However, drought in early growth (1-5 MAP) reduced the storage root yield of cassava by more than 32% (Connor and Cock, 1981). The difference observed in rainfall and its distribution at the early growth stages in 2016/2017 and 2017/2018 was large. Year/season could have contributed to the largest portions of water use efficiency of root yield and biomass production. While reduced canopy size and stomatal closure directly moderate water losses by the crop, reduced crop duration effectively reduces the amount of rainfall received by the crop.

#### 4.5 CONCLUSION

This study assessed the variation in the pattern of soil moisture extraction and water use efficiency of root yield and biomass production of four cassava landraces grown over 2 seasons in Thohoyandou, Limpopo Province, South Africa. Seasonal water use and WUE were not significantly affected by landraces in 2017/2018 but WUE varied with landraces in 2016/2017. The results did not show variability in soil moisture extraction among the landraces. Higher water use in 2016/2017 has led to higher WUE and root yield compared 2017/2018 cropping season. In the current study, it was generally observed that water use efficiencies were greater in ACC#3 and ACC#1, hence these landraces could be better adapted for cultivation in areas with limited water availability than the other landraces. The variation in WUE<sub>r</sub> and WUE<sub>b</sub> between season I and II was not expected, however, variation could be due to rainfall received. Yield was shown to decrease in response to limited water availability while WUE of biomass production was relatively

high in 2017/2018. However, more research is needed to identify more sources of genetic variation in cassava which will enable breeding programs to develop new varieties with high water use efficiency because WUE varies with genotypes and the environment.

## CHAPTER 5: GENOTYPIC VARIATION IN GASEOUS EXCHANGE AND CHLOROPHYLL FLUORESCENCE OF CASSAVA LANDRACES UNDER RAIN-FED CONDITION.

### ABSTRACT

Photosynthesis and water use during early vegetative growth are important physiological traits determining the yield of cassava, but there is limited information currently available for gaseous exchange on cassava in the dry environments of South Africa. Gaseous exchange, PAR, chlorophyll content and chlorophyll fluorescence of four cassava landraces (ACC#1, ACC#2, ACC#3 and ACC#4) grown under rain-fed, were investigated in 2016/2017 and 2017/2018 cropping season in Thohoyandou, South Africa. The experiment used a randomized complete block design (RCBD) with three replications. Gas exchange parameters were determined between 248 and 262 DAP using a LI-6400 portable photosynthesis system infrared gas analyser (LiCor, Lincoln, NE, USA), chlorophyll content was determined between 180 and 311 DAP using chlorophyll content meter (CCM-200 PLUS, Opti-Sciences, Tyngsboro, Massachusetts). Photosynthetic active radiation (PAR) was measured at 7-day intervals starting from 126 DAP until harvest 311 DAP in the 2017/2018 cropping season using AccuPAR, model LP-80 ceptometer (Decagon Devices Ltd., Pullman, USA). Chlorophyll fluorescence measurements were determined between 248 and 262 DAP using a portable pulse amplitude modulation fluorometer (PAM- 2000, Walz, Effeltrich, Germany). Stomatal conductance varied with landraces from 0.08 mmol m<sup>-2</sup> s<sup>-1</sup> (ACC#4) to 0.2 mmol m<sup>-2</sup> s<sup>-1</sup> (ACC#2) and maximum quantum efficiency of PSII ( $F_v/F_m$ ) varied with landraces from 0.652 (ACC#4) to 0.792 (ACC#3) in 2017/2018 cropping season. The proportion of intercepted radiation varied with landraces from 22.62% (ACC#4) to 86.45% (#ACC#3). Chlorophyll content varied with landraces from 33.1 CCI (ACC4) to 55.4 CCI (#ACC3) and from 36.9 CCI (ACC4) to 78.7 CCI (#ACC3) in both seasons. Genotypic variation was observed during the seasons in which ACC#3 had the highest and ACC#4 the lowest mean photosynthesis rate, photosynthetic active radiation, chlorophyll content and maximum photochemical quantum yield of PSII ( $F_v/F_m$ ). Present findings indicated that seasonal dry periods could considerably alter onset physiology and reduce crop growth and yield. However, further investigation needs to be conducted to make definite conclusions.

**Keywords:** Cassava landraces, climatic factors, maximum quantum efficiency of PSII, photosynthetic performance.

## 5.1 INTRODUCTION

Cassava is a tropical crop and has become one of the dominant starchy staple food in the tropical and subtropical regions of Latin America, Asia, and Africa. It is mainly cultivated on small farms in a variety of infertile soils and environments subjected to varying periods of drought stress (Santanoo et al., 2019). Cassava is commonly known for its tolerance to drought stress and high photosynthetic rate El-Sharkawy (2007) irrespective of the cultivar used. Despite this ability, water stress still reduces its net biomass production greatly below its maximum yield potential. Crop yield is primarily determined by photosynthesis in cassava and other fields crops (Furbank et al., 2015; De Souza et al., 2016) and net photosynthetic rate ( $P_N$ ) of cassava leaves was reported to have a significant correlation with storage root yield across environments (El-Sharkawy et al., 2008; Santanoo et al., 2019). Related photosynthesis parameters such as internal  $CO_2$  concentration ( $C_i$ ) are also significantly correlated with root yield of cassava (De Tafur et al., 1997; Zhang et al., 2014; De Souza et al., 2016). Studies have shown that decreases in stomatal conductance mainly reduced the transpiration rate ( $E$ ), and photosynthetic rate (Yan et al., 2016).

Although cassava can withstand drought, Oyetunji et al. (2007) reported a decrease in cassava chlorophyll content during water stress conditions. A decrease in chlorophyll synthesis has a detrimental effect on the quantum yield of PSII of cassava and consequently affects its yield performance because the quantum yield of PSII in plants can be directly related to their stress physiology. The relative quantum yield of PSII can change with abiotic factors such as water deficit, solar radiation and temperature (Vongcharoen et al., 2019). Therefore, quantifying the quantum yield of PSII can provide important information about the plant-environment relationship.

Photosystem II (PSII) is a sensitive component to heat stress (Baker and Rosenqvist, 2004). The maximum quantum efficiency of PSII ( $F_v/F_m$ ) provides an estimate of the maximum quantum efficiency of PSII, which is primarily affected by heat stress and a healthy leaf generally gives an  $F_v/F_m$  value of about 0.75 to 0.80 (Zhou et al., 2015; Murchie and Lawson, 2013). Photosynthetic performance of cassava leaves can quickly change during the day depending on the fluctuation in environmental factors, particularly the light intensity (Vitolo et al., 2012). Photosynthetic capacity depends on both the efficiency of light-use and net  $CO_2$  fixation reactions (Parry et al., 2011). The efficiency of the light-dependent reaction is largely indicated by the measurement of effective quantum yield of PSII photochemistry ( $\Phi_{PSII}$ ) which determines the relative electron transport rate (ETR) (Flood et al., 2011). The net photosynthetic rate depends on stomatal and non-stomatal factors which are in turn controlled by external environmental factors and biochemical characteristics of plant cells (Saibo et al., 2009). Variation in  $\Phi_{PSII}$  is largely



controlled by light intensity, being lowered with increasing photosynthetic active radiation (Hazrati et al., 2016).

There is hardly any information on the gaseous exchange performance and chlorophyll fluorescence of cassava landraces conducted in Southern African including South Africa. Information on environmental effects in different seasons on photosynthetic performance and chlorophyll fluorescence of cassava landraces is seriously lacking in the region. With this study, we intend to use quantum yield of PSII photochemistry ( $\Phi_{PSII}$ ) and quantum efficiency of photochemistry of photosystem II ( $F_v/F_m$ ) to identify the responses cassava landraces that are adapted to the warm conditions in the north-eastern part of South Africa and maintenance of higher root yield under a warming climate and as genetic resources for a breeding programme.

It was hypothesised that there was variation in gaseous exchange, the quantum yield of PSII photochemistry, PAR and chlorophyll content of four cassava landraces. Therefore, this study investigated the variation in gaseous exchange, the effective quantum yield of PSII photochemistry, photosynthetic active radiation (PAR) and chlorophyll content of four cassava landraces grown under the rain-fed condition in Thohoyandou, a representative location of the dry environment of north-eastern South Africa.

## 5.2 MATERIALS AND METHODS

Each chapter has more specific materials and methods including formulas. The study site, experimental design, treatments that were evaluated and agronomic practices are described in detail in Chapter 3.

### 5.2.1 Data collection

Gas exchange variables including net photosynthetic rate ( $P_N$ ), transpiration rate ( $E$ ), stomatal conductance ( $g_s$ ) and intercellular  $CO_2$  concentration ( $C_i$ ) were measured at  $CO_2$  concentration of  $400\mu\text{molmol}^{-1}$  using a LI-6400 portable photosynthesis system infrared gas analyser (LiCor, Lincoln, NE, USA) with an automatic cuvette of up to  $6\text{cm}^2$  leaf area. Measurements were taken from five fully expanded young healthy plant leaves that were allowed to equilibrate to  $20^\circ\text{C}$  cuvette conditions, the flow rate at  $500\mu\text{mol s}^{-1}$  and PPFD of ca  $1000\mu\text{molm}^{-2}\text{s}^{-1}$  for 3 minutes. Data were collected on four plants daily during the stress period between 0900 h and 1200h at the vegetative and flowering growth stages. The leaf chamber was clamped over the middle portion ( $6.25\text{cm}^2$  surface area) of the central lobe of the measured youngest expanded matured leaves and held toward the sun for 30 to 60 s to obtain steady-state gas exchange rates. Photosynthetic photon flux density and leaf temperature were measured with a silicon photodiode and thermocouple respectively, both housed within the 0.25 L cuvette of the IRGA. Gas exchange measurements were taken under natural conditions of air temperature, incident photosynthetic photon flux density (PPFD),  $CO_2$  concentration, and vapour pressure deficit (VPD). Under natural conditions, air temperature and VPD values within the cuvette were maintained close to those of the ambient air. The leaf chamber was held at right angles to incident radiation to prevent shading inside the curvette. Instantaneous water use efficiency was calculated as the ratio of net photosynthetic rate ( $P_N$ ) to transpiration rate ( $E$ ) ( $WUE = P_N/E$ ).

Chlorophyll content was determined from five previously selected and tagged leaves in each plot using chlorophyll content meter (CCM-200 PLUS, Opti-Sciences, Tyngsboro, Massachusetts) between 09h00 and 12h00 each occasion. To measure the chlorophyll content, the central lobe of the healthy leaves was placed in the chamber of the meter and pressed to close. The meter was calibrated after each measurement to ensure accuracy. CCM-200 Plus uses transmittance to estimate the chlorophyll content in leaf tissue. Two wavelengths (940 and 665nm) are used for absorbance determinations.

The proportion of radiation intercepted ( $F_i$ ) by the canopy was approximated based on the method presented by Gallagher and Biscoe (1978) as shown in equation 5.2 below.

$$F_i = 1.0 - T_i \quad (5.2)$$

Where  $T_i$  is a fraction of incident radiation transmitted by the canopy i.e:

$$T_i = 1 - \frac{\text{PAR below canopy}}{\text{PAR above the canopy}} \quad (5.3)$$

The total amount of photosynthetically active radiation (PAR) intercepted ( $IR$ ) was approximated following the method used in earlier studies (Anwar et al., 2003; Jahansooz et al., 2007).

$$IR = F_i * S_i \quad (5.4)$$

Where  $S_i$  is the total incident radiation.

PAR was measured at 7-day intervals starting from 126 DAP until harvest 311 DAP in the 2017/2018 cropping season. The measurements were taken between 10.00 hours and 13.00 hours on clear, cloudless days using AccuPAR, model LP-80 ceptometer (Decagon Devices Ltd., Pullman, USA). When taking the measurements, the ceptometer was placed horizontally above the canopy when measuring PAR above the canopy. When measuring PAR below the canopy, the ceptometer was positioned between the rows in such a manner that it ran perpendicular to the rows. PAR was taken as 50% of the incident solar radiation (Monteith and Unsworth, 1990).

Chlorophyll fluorescence measurements were taken with a portable pulse amplitude modulation fluorometer (PAM- 2000, Walz, Eifeltrich, Germany) following the procedure outlined by Baker and Rosenqvist (2004). Leaf chlorophyll fluorescence values, such as the effective quantum yield of PSII ( $\Phi_{PSII}$ ), maximum photochemical efficiency of photosystem II  $F_v/F_m$  ( $F_v = F_m - F_o$ ), minimum fluorescence ( $F_m$ ) and variable fluorescence ( $F_v$ ) were taken between 28 June and 12 July 2016/2017 on the youngest, fully expanded leaf using a PAM2100 portable chlorophyll fluorometer (Walz, Eifeltrich, Germany) and in 2017/2018 cropping season. Five plants from each of the twelve plots were selected from the four inner-most rows, clamped on using light-exclusion clips (Walz, Eifeltrich, Germany) and readings recorded. The operating efficiency of PSII ( $F_q/F_m'$ ) (where  $F_q = F_m' - F$ ) and leaf temperature readings were taken and recorded during the day between 0800h and 12h00 noon on five selected plants from each of the sixteen plots from the four innermost rows with the fiber optics attached to leaf clip holder 2030-B (Walz, Eifeltrich, Germany).

All data were subjected to one-way analyses of variance (ANOVA) using GenStat 18<sup>th</sup> Edition based on Randomized Complete Block Design. Means were separated using the standard error of difference (S.E.D) when F-test indicated significant differences among the treatments.

### 5.3 RESULTS

Mean temperatures and vapour pressure deficit recorded during data collection in July 2017. The values of mean leaf temperature ranged between 23.61 to 24.12 °C to and for vapour pressure deficit (VPD) was between 1.53 to 1.63 KPa, respectively.

Table 5.1: Mean temperatures and vapour pressure deficit recorded during data collection in July 2017

Genotypes	Mean leaf temperature (°C)	Mean vapour pressure deficit (Kpa)
ACC#1	23.61	1.53
ACC#2	23.52	1.45
ACC#3	24.14	1.63
ACC#4	23.31	1.42



### 5.3.1 Gaseous exchange parameters

There was no variation in photosynthetic rate amongst the landraces but landraces affected stomatal conductance (Table 5.2). Stomatal conductance varied ( $P < 0.05$ ) with landraces from  $0.08 \text{ mol } H_2O \text{ m}^{-2} \text{ s}^{-1}$  (ACC#4) to  $0.2 \text{ mol } H_2O \text{ m}^{-2} \text{ s}^{-1}$  (ACC#2).

Table 5.2. Genotypic variation in net photosynthetic rate ( $P_N$ ), Transpiration rate (E), Stomatal conductance ( $g_s$ ), Intracellular  $CO_2$  concentration ( $C_i$ ) and Instantaneous water use efficiency (iWUE) in 2016/2017.

Genotypes	$P_N$ ( $\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$ )	E ( $\text{mmol } H_2O / \text{m}^{-2} \text{ s}^{-1}$ )	$g_s$ ( $\text{mol } H_2O / \text{m}^{-2} \text{ s}^{-1}$ )	$C_i$ ( $\mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$ )	iWUE ( $\mu\text{mol } CO_2 / (\text{mmol } H_2O)$ )
ACC#1	11.0	1.60	0.10 <sup>a</sup>	274.0	8.20
ACC#2	10.30	1.10	0.20 <sup>ab</sup>	226.40	7.91
ACC#3	11.10	2.0	0.10 <sup>a</sup>	262.70	8.49
ACC#4	10.0	1.40	0.08 <sup>c</sup>	234.30	7.34
F (p ratios)	ns	ns	**	ns	ns
S.E.D	0.849	0.2418	0.0305	21.07	1.514
CV (%)	9.80	19.1	18.2	18.2	18.3

\*= $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\*= $P < 0.001$  and ns = not significant. C.V= coefficient of variation



There was no genotypic variation in effective quantum yield among the landraces. Leaf temperature varied ( $P < 0.01$ ) with landraces from 26.56 °C (ACC4) to 28.33 °C (#ACC1) (Table 5.2).

Table 5.3: Genotypic variation in chlorophyll fluorescence parameters of four cassava genotypes grown in the 2016/2017 cropping season.

	Temperature (° C)	Quantum yield of photochemistry II (ΦPSII)	Temperature (° C)	Quantum yield of photochemistry II (ΦPSII)	Temperature (° C)	Quantum yield of photochemistry II (ΦPSII)
	248 DAP		256 DAP		262 DAP	
Genotype						
ACC#1	27.76 <sup>a</sup>	0.34	27.45	0.41	28.33	0.44
ACC#2	27.26 <sup>b</sup>	0.34	27.42	0.36	28.67	0.43
ACC#3	28.33 <sup>ab</sup>	0.35	27.91	0.38	28.89	0.47
ACC#4	26.26 <sup>c</sup>	0.28	26.75	0.35	28.49	0.39
F-ratio	**	ns	ns	ns	ns	ns
S.E.D.	0.356	0.045	0.862	0.040	0.562	0.060
CV (%)	1.6	16.8	3.9	13.1	2.40	16.9

\*= $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\*= $P < 0.001$  and ns = not significant. C.V= coefficient of variation

The proportion of intercepted radiation was affected by landraces in 2017/2018 cropping season. Highest proportion of intercepted radiation was observed in ACC#3 and the lowest in ACC#2. Proportion of intercepted radiation varied with landraces from 22.62% (ACC#2) to 86.45% (#ACC#3) measured between 80 and 300 DAP.

### 5.3.2 The proportion of the photosynthetically active radiation

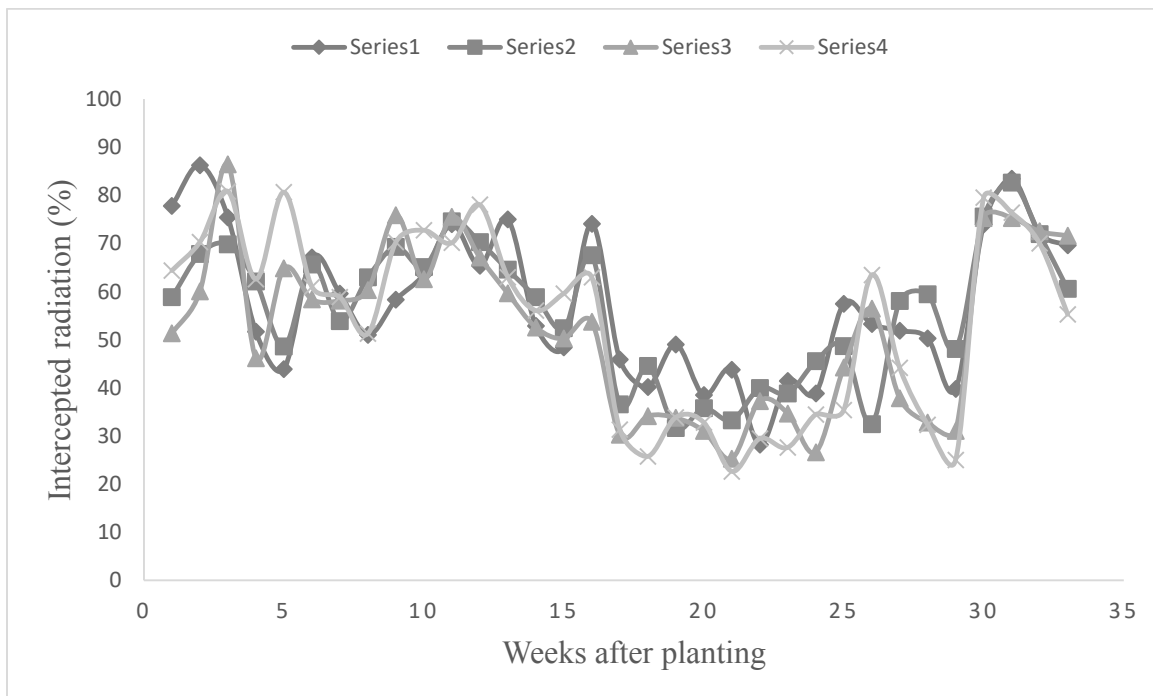


Figure 5.1: Genotypic variation in the proportion of intercepted radiation amongst the landraces in the 2017/2018 cropping season.

### 5.3.3 Chlorophyll content

There were significant genotypic variations in chlorophyll content recorded in both season between 180 and 311 DAP. Chlorophyll content varied with landraces from 33.1 CCI (ACC4) to 55.4 CCI (#ACC3) in the 2016/2017, and in 2017/2018 cropping season chlorophyll content varied with landraces from 36.9 CCI (ACC4) to 78.7 CCI (#ACC3). The highest genotypic variation in chlorophyll content was observed in ACC#3 whilst the lowest chlorophyll content was recorded in ACC#4 in both seasons.

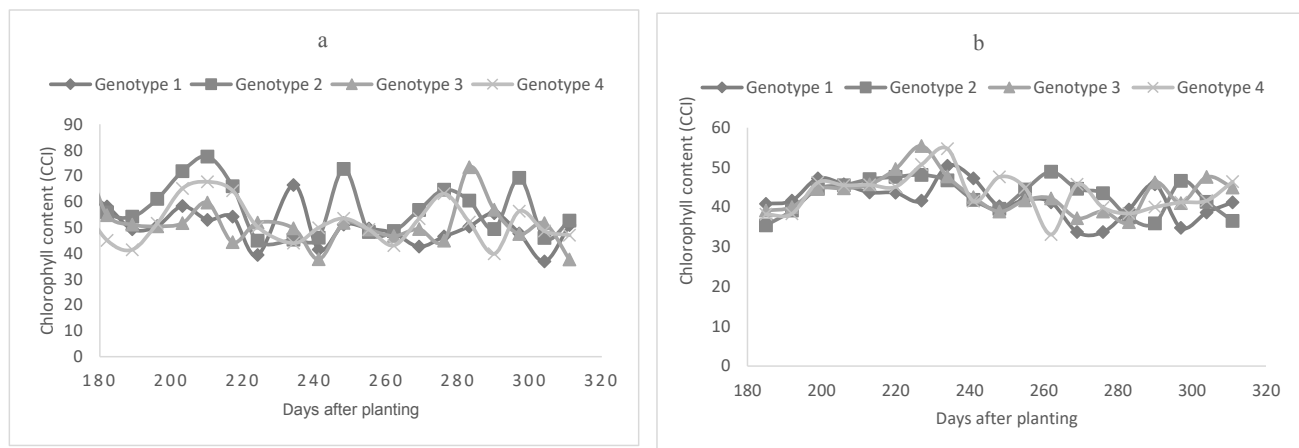


Figure 5.2: Genotypic variation in chlorophyll content index (CCI) amongst cassava landraces grown under rain-fed condition in 2016/2017 (a) and 2017/2018 (b) cropping season.





### 5.3.4 Chlorophyll fluorescence

There was no variation in the effective quantum yield of photochemistry II amongst the landraces in 2016/2017 cropping season but genotypes affected variable minimal fluorescence yield of dark-adapted state ( $F_o$ ) and maximum quantum efficiency of PSII ( $F_v/F_m$ ) in 2017/2018 cropping season (Table 5.3). Effective quantum efficiency of PSII ( $\Phi_{PSII}$ ), values ranged from 0.63 (ACC#3) and 0.55 (ACC#4). Similarly, minimal fluorescence yield of dark-adapted state ( $F_o$ ) was greater in ACC#3 (1372) and ACC#1 (1253) compared to ACC#2 (1214) and ACC#4 (1127), (Table 5.3.4). In contrast, minimal fluorescence yield of dark-adapted state ( $F_o$ ) and maximum quantum efficiency of PSII ( $F_v/F_m$ ) were greater in ACC#3 (1372 and 0.80, respectively).

Table 5.4. Variation in mean chlorophyll fluorescence parameters of both light and dark-adapted leaf amongst cassava landraces.

Season/Year	2017/18 (Light)			2017/18 (Dark)		
	Minimal fluorescence ( $F_o$ )	Effective quantum yield of PSII ( $\Phi_{PSII}$ )	Maximum primary yield of photochemistry I ( $F_v/F_o$ )	Minimal fluorescence ( $F_o$ )	Maximum primary yield of photochemistry I ( $F_v/F_o$ )	Maximal quantum yield of PSII ( $F_v/F_m$ )
Genotype						
ACC#1	310.00	0.57	1.03	1253.00 <sup>ab</sup>	3.52	0.79 <sup>a</sup>
ACC#2	321.00	0.52	1.03	1212.00 <sup>c</sup>	3.92	0.75 <sup>c</sup>
ACC#3	357.00	0.63	1.35	1372.00 <sup>a</sup>	4.34	0.80 <sup>a</sup>
ACC#4	294.00	0.55	1.38	1127.00 <sup>b</sup>	3.62	0.66 <sup>d</sup>
F-ratio	ns	ns	ns	*	ns	*
S.E.D.	48.8000	0.0862	0.4450	58.9000	0.1693	0.0384
CV (%)	18.6	19.2	14.5	5.8	11.4	6.3

## 5.5 DISCUSSION

Low rainfall is an important environmental constraint that affects all physiological processes involved in the growth and development of plants. This influence would be a set of responses to low rainfall and high temperatures mainly affecting the mechanism of gas exchanges (Centritto et al. 2009). In this study, we can better understand how these mechanisms work in cassava in the semi-arid environment, in order to generate information on chlorophyll fluorescence regulation for carbon gain, and water use efficiency, which are important characteristics for the maintenance of the plant photosynthetic capacity.

Gas exchange data indicated that the tested cassava landraces have a lower carbon dioxide assimilation rate compared to other cassava genotypes. Net photosynthetic rate ranged between 10.0 and 11.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Table 5.2) compared to maximum photosynthesis values of 42 and 50  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for cassava genotypes grown in Colombia (El-Sharkawy et al. 1992; El-Sharkawy and De Tafur., 2010). However, in the current study, internal  $\text{CO}_2$  was within the reported range despite a reduction in net photosynthetic rate, stomatal conductance and the rate of transpiration (Table 6.2). This result implies that the restriction of  $\text{CO}_2$  diffusion from the outside air into the chloroplast during winter was one of the factors responsible for lower photosynthesis. However, the ability of ACC#1 and ACC#3 to maintain a higher growth and photosynthetic rate can potentially be attributed to higher electron transport under drought stress (Vitolo et al., 2012).

The high carbon dioxide is an indication that net photosynthetic rate, stomatal conductance, and transpiration were pre-dominantly reduced by non-stomatal limitation such as low temperature in winter (Vongchareon, et al., 1971; El-Sharkawy, 2006; Santanoo et al., 2019). It is also clearly indicating that in addition to lower stomatal conductance, low water use may have decreased the enzymatic activities associated with photosynthetic carbon metabolism, a common effect in plants grown under dry condition (Hazrati et al., 2016). In the current study, internal  $\text{CO}_2$  was lower and could have contributed greatly to stomatal conductance hence the low net photosynthesis rate. The reduction in stomatal conductance in response to low temperature and soil moisture depletion could partly be responsible for the reduced photosynthetic rate. Photosynthetic rates of the current study are comparable to several cassava genotypes from Nigeria which ranged between 5 – 15  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Indira et al., 2007). Similarly, De Tafur et al (1997b) reported cassava net photosynthesis that ranged between 7  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and 20  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the semi-arid zone of Colombia. High photosynthetic rates recorded in ACC#1 and ACC#3 could be possibly a means of maximising carbon uptake while minimising water loss during the time of high evaporative demand.

High *i*WUE in ACC#1 and ACC#3 could be due to a lower transpiration rate as a result of partially closed stomata in response to dry air (Table 5.2). The high *i*WUE of ACC#1 and ACC#3 could be attributed to efficient control of stomatal conductance ( $0.1$  and  $0.1 \text{ mol } H_2O / m^{-2} \text{ s}^{-1}$ ) resulting in high *A* ( $11.0$  and  $11.0 \mu\text{mol } CO_2 \text{ m}^{-2} \text{ s}^{-1}$ ). Important physiological traits for improving WUE at the leaf level is the net photosynthetic rate and stomatal conductance. Therefore, the selection of cassava landraces with a higher stomatal conductance may lead to improved WUE and photosynthetic rate (Condon et al., 2002; Gilbert et al., 2011). Increased WUE enables the absorption of carbon despite reduced water loss (Vitolo et al., 2012, Bertolli and Souza, 2013).

Cassava photosynthetic rate varies greatly largely due to variation in climate, soil, genotypes as well as management practices. It is noteworthy that even when water is not limiting factor photosynthesis can be reduced. The survival of a plant in a drought environment depends largely upon its ability to photosynthesize and to maintain positive water balance (Wuenscher and Kozlowski, 1971) but this may vary with genotypes and environment. The photosynthetic capacity of leaves depends on the characteristics and amounts of the components of the photosynthetic machinery, the production of which depends on the availability of water, light, temperature, and nutrients (El-Sharkawy, 2012).

Previous studies reported an optimum temperature range for cassava photosynthesis in tropical environments between  $30\text{-}35 \text{ }^\circ\text{C}$  (El-Sharkawy, 2007; El-Sharkawy, 2012). The lower net photosynthetic rate in this study could be due to low leaf temperature ( $26.6 \text{ }^\circ\text{C}$  to  $28.9 \text{ }^\circ\text{C}$ ) since measurements were taken during winter, hence low photosynthetic rate (Table 5.1). However, during winter season, when temperatures were low, soil moisture content was low. Cold stress adversely affects plant growth and development. Low temperature has been regarded as major stress for crops, and its negative effects have been studied extensively (Pompodakis et al., 2005; Repo et al., 2004; Santanoo et al., 2019; Phoncharoen et al., 2019). Although cassava can be widely adapted to different environments it usually requires a warm climate with high solar radiation for optimum photosynthesis, growth, and productivity (El-Sharkawy, 2012).

The down-regulation of photosynthesis causes an energy imbalance in photosystem II, which results in photoinhibition (Murchie and Lawson, 2013). Santanoo et al. (2019) reported a decrease in photosystem II efficiency in cassava genotypes under water stress. Photosystem efficiency (*Fv/Fm*) helps in the detection of any damage to photosystem II and its probable inhibition. Low rainfall and high temperatures affects photosystem efficiency and thus, decreases the electron transport rate and the effective quantum yield of photosystem II (Flexas

et al., 2002). Quantum yield of photosystem II was reduced in cassava due to low temperature and soil moisture content in 2016/2017 cropping season during winter (Figure 3.2).

Water and heat stress could have attributed to reduction of chlorophyll content, which in turn alters their light harvesting capabilities (Farooq et al., 2009). Breatic and Zivcak (2013) pointed out that low rainfall couple with high temperatures decreases chlorophyll content binding proteins and, in effect, impairs the synthesis of chlorophyll content, thus leading to a reduction in light harvesting pigment protein associated with photosystem II. The thylakoid membrane emits chlorophyll fluorescence and it can be used as a proxy for photosynthetic reaction in photosystem II (Ahmed et al., 2002). Damage to the light reaction systems in photosynthetic apparatus as a result of high temperatures and low rainfall can be detected by analysing chlorophyll fluorescence and photosynthetic efficiency (Sawatraksa et al., 2018).

Although there was no significant variation in quantum yield of photosystem II in both seasons, there was variation in quantum efficiency of photosystem II ( $F_v/F_m$ ) in 2017/2018. The quantum efficiency of photosystem II ( $F_v/F_m$ ) was maximal (0.80) when recorded during 2017/2018 cropping season. The literature reports that plants under absence of stress show potential quantum yield ( $F_v/F_m$ ) in the range from 0.75 to 0.85 (Björkman and Demmig, 1987; Bolh r-Nordenkamp et al., 1989). However, the quantum yield of photosystem II values which was observed in 2016/2017 cropping season were below that range, reflect photoinhibitory damages in the reaction centers of photosystem II.

The obtained results allow inferring that, under the experimental conditions, the low temperatures in winter and low soil water content caused damages to the photosynthetic apparatus of the landraces a fact evidenced by the reduction in the quantum yield of PSII, 0.39. Cruz et al. (2013) observed that the lowest value in the  $F_v/F_m$  ratio was 0.320 in cassava cultivars under low soil water content and temperature, recovering with subsequent rainfall. (Ekanayake et al. (1998) report that plants subjected to salinity have low quantum yield, probably due to stomatal closure and decrease in photosynthesis, physiological mechanisms that may have occurred with the plants subjected to water or temperature stress in this experiment. Lower  $F_v/F_m$  and quantum yield of photosystem II among the landraces also indicated enhancement of the photoinhibition (Oyetunji et al., 1998; Baker 2008, Gorbe and Calatayud 2012).

Decreases in photosynthetic activity are paralleled by a reduction in leaf quantum yield of photosystem II and  $F_v/F_m$  (Ekanayake *et al.*, 1998), and leaf chlorophyll content is often indirectly associated with growth and yield of cassava (Ekanayake *et al.*, 1996; Oyetunji *et al.*, 1998).

In the 2016/2017 cropping season, all the landraces recorded lower than the published value of 0.862 (Santanoo et al., 2019) for non-stressed plants. Non-photochemical quenching (NPQ) processes help to regulate and protect photosynthesis in environments in which light energy absorption exceeds the capacity for light utilisation. The  $F_v/F_m$  value in the dark measures the maximum efficiency of PSII when all PSII centers are open and are widely used as an indicator of photoinhibition caused by photodamage to PSII (Baker 2008, Gorbe and Calatayud 2012). High chlorophyll fluorescence values indicate high quantum efficiency of photochemistry and heat dissipation that increase crop photosynthesis and root yield (El-Sharkawy and de Tafur, 2010; Murchie and Lawson, 2013).

Reduced photosynthetic rates in winter when soil moisture content was low have also been directly linked to water use efficiency, with stomatal closure noted to result in increased water use efficiency (Murchie and Lawson, 2013), with the tool noted to be very critical in assessments of phenotypic variations within large drought stress tolerance breeding pools. However, the lower effective quantum yield of PSII observed in the season I compared to season II could be due to the effect of low temperature as well as low soil moisture content as the values were measured in winter (June). Studies have shown the negative effects of low temperature (in winter) on the reduction of quantum yield of PSII and ultimately yield in roses and other field crops (Pompodakis et al., 2005) and temperate bamboo (Van Goethem et al., 2013).

Reduction in intracellular  $CO_2$ , due to stomatal closure, results in reduced substrate availability for photosynthesis. Therefore, there is need to down-regulate photosynthesis in line with reduced substrate availability. In this regard, chlorophyll content has been shown to decrease in limited moisture conditions (Li et al. (2004)), for example, in barley (Anjum et al., 2003, wheat Zaharieva et al., 2001; Izanloo et al., 2008). (Kiani et al., 2008). The significant differences between landraces in both seasons could have attributed sensitivity to moisture stress especially in 2017/1028 (Table 4.1). The higher CCI recorded in ACC#3 in both season showed the variability that exists within landraces, with respect to responses to water stress.

Research has reported that reduction in the rate of transpiration, stomatal closure and decrease in the flow of carbon dioxide into leaves, ultimately leads to a decline in net photosynthesis resulting in reduced plant growth. Decrease in carbon uptake is regulated by stomatal conductance and it has a great influence on photosynthesis and chlorophyll. The results of this study showed that chlorophyll content was lower in 2017/2018 compared to 2016/2017. The pattern of chlorophyll content was the same in all the landraces, which means the landraces responded the same to the prevailing climate. However, in 2017/2018 the reduction in chlorophyll content, probably resulted in less energy captured for photosynthesis.

If this down-regulation was not to occur, the plant would have more energy than required to fix carbon dioxide resulting in increased levels of free radicals which would in turn damage the chloroplast membranes (Chaves and Oliveira, 2004). As such, cassava landraces demonstrated an ability to down-regulate photosynthesis in line with reduced carbon dioxide availability caused by stomatal closure. Several experiments conducted on cassava (Nguyen et al., 1997; Lahai and Ekanayeka, 2010; Aspiazu et al., 2010) and barley (Anjum et al., 2003) also showed that low rainfall decreased chlorophyll content.

## **5.6 CONCLUSION**

Overall, the results show that chlorophyll fluorescence parameters, PAR and chlorophyll content for ACC#1 and ACC#3 were high and the landraces recorded high root yield in both seasons. The combination and advantages of these factors suggest that these landraces have a better adaptive advantage to be grown in water-limited condition. Low temperatures rapidly decrease leaf conductance leading to a decrease in CO<sub>2</sub> uptake and transpiration. Lower WUE recorded in ACC#2 and ACC#4 in winter was probably caused by evapotranspiration stress due to reduced soil moisture. In contrast, the high WUE recorded in ACC#1 and ACC#3 may be a trait contributing to increased quantum yield under stress conditions. This indicated that ACC#1 and ACC#3 grown in this climate had an efficient photo-protection mechanism and did not suffer from chronic photo-damage showed high photosynthetic efficiency.

## CHAPTER 6: GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATIONS

### 6.1 General conclusion

Poor and erratic rainfall experienced in the northeastern region of South Africa is a major constraint to rain-fed cassava production. The adoption of strategies to ensure the effective and efficient use of stored soil water by rain-fed cassava in this environment is paramount for ensuring enhanced and sustainable production of the crop. Growing cassava landraces that have high water use efficiency can sustain yield under limited water environments is a better option. However, the challenge remains because water use efficiency is a complex trait and not an easy target for plant breeders. This breeding challenge is overcome by identifying secondary traits that are highly heritable and simple to work with as surrogates. A combination of improved genotypes and management options can help increase water use efficiency and sustain yields under water-limited conditions. Therefore, this study determined variation in water use efficiency, gaseous exchange and yield of four cassava landraces grown in the dry environment of Limpopo Province, South Africa.

The results from this study showed that landraces affected root yield and yield component, chlorophyll content, stomatal conductance and pattern of water use in 2016/2017 but not in 2017/2018 cropping season. There was an increase in root yield and water use with rainfall received. An increase in root yield and yield components was associated with greater water use and high rainfall received in 2016/2017. Limited water availability has been reported to result in reduced plant growth due to impairment of cell division and expansion hence yield (Okogbenin et al., 2003). The greater water use and high rainfall received could be associated with a significant variation in number of roots per plant, mean root weight, aboveground biomass, root girth, root length, and harvest index; this implies that high root length coupled with increased root size could have resulted in yield improvement in 2016/2017 compared to 2017/2018 cropping season as early observed by Aina et al (2007). The significant positive correlation between root yield, water use efficiency of root yield and biomass production of cassava between the two seasons, this means that the more water was used efficiently for root yield translocate, hence yield is improved in 2016/2017 compared to 2017/2018.

Water use efficiency (WUE) is an important crop index which can be used to assess how soil water has been used efficiently for total biomass production and economic yield production. Water use efficiency (WUE) of cassava has also been used to evaluate in moisture limiting conditions (Okogbenin et al., 2013). In the current study both ACC#1 and ACC#3 were efficient in the use of soil water for root yield and biomass production during the growing period as they used different amount of soil water to produce different levels of yield and biomass. The results from current study are comparable to the findings by Brown et al (1989) on chickpea who

reported greater water use efficiency with low water use. In contrast, the results from this current study were not in line with the results reported by Odubanjo et al. (2011) and Polthanee and Srisutham, (2018) who found higher WUE in rain-fed conditions compared to irrigated conditions. Similarly, the higher rainfall and increase in root yield which was significant in 2016/2017 could have contributed to the increase in WUE of root yield. The results of the current study were not expected, because crops grown under limited moisture tend to have greater water use efficiency than crops that receive water. Although there was hardly any significant variation in water use, there were significant positive correlation between root yield, water use efficiency of root yield and biomass production of cassava between the two seasons.

Greater use water was recorded and water use efficiency of root yield was recorded in 2016/2017 compared to 2017/2018 cropping season, and it was attributed to rainfall received. Cassava is mostly grown on stored soil moisture by small scale farmers who cannot afford irrigation, it is important to make management decisions that ensure moisture is conserved. The use of landraces with a greater pattern of moisture extraction could provide such a path for soil moisture conservation under receding moisture conditions and maybe a helpful management option for cassava. The most water-efficient genotypes can be used as parents in a breeding program to increase WUE or grown directly by growers. The observed genotypic variation for WUE was generally high and there is a need to identify more sources of genetic variation in cassava which will enable breeding programs to develop new varieties with high water use efficiency because WUE varies with genotypes and the environment.

Chlorophyll is one of the major chloroplast components for photosynthesis (Manivannan et al., 2007). Chlorophyll and its associated accessory light receptor pigments (xanthophyll and carotenoids) was increased by limited moisture. In photosynthesis, chlorophyll is the principal light receptor pigment and its reduction may adversely affect photosynthetic rate. Both ACC#1 and ACC#3 recorded high chlorophyll content in both seasons, which showed that both landraces had a high photosynthetic capacity hence high water use, water use efficiency and yield potential. Although, high values of chlorophyll content were observed in the drier season than the wetter season. Same results were reported by Arunyanark et al. (2008) who observed stable chlorophyll content under drought in groundnut. Lahai et al. (2003) also related root yield in cassava genotypes with increased concentration of leaf chlorophyll under moisture stress but this has not been fully exploited in cassava yield improvement under moisture stress based on leaf chlorophyll content stability.



The reduction in stomatal conductance in response to low temperature and soil moisture depletion could partly be responsible for the reduced photosynthetic rate and quantum yield. High chlorophyll fluorescence values indicate high quantum efficiency of photochemistry and heat dissipation that may increase crop photosynthesis and biomass (Murchie and Lawson, 2013). However, the lower effective quantum yield of PSII observed in the season I compared season II could be due to the effect of low temperature as well as low soil moisture content as the values were measured in winter (June). These results are comparable with the results reported by Pompodakis et al. (2005) and Van Goethem et al. (2013) who reported the negative effects of low temperature (in winter) on the reduction in photosynthetic rate and quantum yield of PSII in roses and temperate bamboo, respectively. Stomatal closure and the subsequent reduction in water loss prevented damage to the photosystems. However, an increase in WUE may be interpreted as an adaptive response to progressive water scarcity during that time. High WUE may be a trait contributing to increased quantum yield hence root yield in both under stress conditions and non-stressed condition.

## 6.2 General conclusion

The results of this research showed genetic variation for WUE but not for water use. The results of this study also clearly indicated that ACC#3 and ACC#1 were able to exploit the more favourable growth conditions in 2016/2107 and thus outperform the other 2 landraces but did not appear to have any yield advantage in the drier cropping season. There was a significant positive correlation between root yield and aboveground biomass (0.847\*\*\*), root girth (0.489\*), weight per root (0.528\*\*), root length (0.750\*\*\*) and harvest index (0.714\*\*\*). There positive correlation between root yield and harvest index in 2016/2017 cropping season suggest that the high yielding landraces (ACC#3 & ACC#1) were able to not only accumulate high crop biomass but to also partition most of the biomass into the storage roots. In general, cassava productivity in the dry environments can be increased by selecting genotypes with high yield potential and high WUE. These genotypes should show drought tolerance and be stable across environments. By targeting secondary traits that confer yield under dry environments, and using them to construct cassava ideotypes which can be coordinated to the growing environment, yield may be increased.

Greater water use in the wetter season improved root yield and water use efficiency of root yield and biomass. Cassava landraces that had high yield potential coupled with WUE performed well in both seasons. In general, cassava productivity in water stressed environments can be increased by selecting landraces with high water use, yield potential and high WUE. These genotypes should show drought tolerance and be stable across

environments. By targeting secondary traits that confer yield under water stressed environments, and using them to construct cassava landraces which can be matched to the growing environment, yield may be increased. Photosynthetic rate did not affect landraces, however stomatal conductance varied with landraces. Overall, our results show that chlorophyll fluorescence parameters and net photosynthetic rate for ACC#1 and ACC#3 were high and the landraces recorded high root yield in both seasons. The combination and advantages of these factors suggest that these landraces have a better adaptive advantage to be grown in water-limited condition. By targeting secondary traits that confer yield under dry environments, and using them to construct cassava ideotypes which can be coordinated to the growing environment, yield may be increased. This study identified ACC#1 and ACC#3 as a better adaptive landrace due to its high water use, photosynthetic rate, water use efficiency and root yield, therefore we recommend further evaluation of the possibility of using the landraces in cassava improvement programmes.

### **6.3 Recommendation**

- 6.3.1 The most water efficient landraces can be used as parents in a breeding program to increase WUE or grown directly by local farmers.
- 6.3.2 We recommend further evaluation of the 2 landraces and its possibility of using the landraces in cassava improvement programmes.
- 6.3.3 Further research is also needed to assess the difference in quantum yield, since in 2016/2017 it was measured in winter only.
- 6.3.4 Further research is needed to identify more sources of genetic variation in cassava which will enable breeding programs to develop new varieties with high water use efficiency because WUE varies with genotypes and the environment.

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