Soil Water Deficit Stress on Bambara groundnut (*Vigna subterranea* [L.] Verdc) and Groundnut (*Arachis hypogaea* [L.])

Aloyce Callist Kundy
MSc Crop Science, BSc Agronomy

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Dedication

To all members of the “three families” I belong. You always encourage and pray for me, you were with me during both up and down situations, and here is our achievement. “Psalm 133”, explains it better.

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Special appreciations are due to the creator almighty GOD.

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Abstract

It is projected that, by year 2100 global population will reach 11.2 billion people. Climate change is projected to increase temperature and reduce water availability. The effects of climate change (e.g. frequent droughts) on crop yields in the world is largely negative. And these effects have resulted to destructing social, environmental and economic problems such as famines, energy crisis, insufficient water supply and ruination of ecosystems. With increasing world population and climate change, strategies to cope with the changing climate cannot be overlooked. Crop intensification and diversification are of first priority. Leguminous crops such groundnut *(Arachis hypogaea* (L.)) (GT) and bambara groundnut (*Vigna subterranea* (L.) Verdc) (BGT) are grown in relatively dry, semi-arid areas and display a suit of drought resistance mechanisms that allow them to produce yield under low rainfall conditions. Although variations in drought resistance exist within species and between species, traits and mechanisms involved are not well studied. Five trials were conducted to study the effects of water deficit stress on GT and BGT landraces. Experiments used split plot in randomized complete block design. Four bambara groundnut landrace-derived genotypes viz NALBAM 2, NALBAM 4, DodR, S19-3 and one groundnut variety, MNANJE, were assigned to subplots and three water regimes to main plots. Water treatments were; well-watered throughout, water stress imposed during flowering and water stress imposed during pod development. Soil water deficit significantly ($p < 0.001$) affected the plants' performance. Flowering stage proved to be more sensitive to insufficient water supply. This means that, by ensuring enough water supply during flowering could improve crop performance under dry areas. Water deficit stress increased proline (µmoles $gram^{-1}$ tissue) content by 123% in stressed plots. Highest percent increase in proline was found in MNANJE (174%) and lowest percentage proline increase in NALBAM 4 (89%). Percentage decrease in the rate of

photosynthesis (µmol CO_2 m^{-2} s^{-1}) ranged between 60% (MNANJE) and 85% (DodR). Water deficit decreased stomatal conductance (molH_20 m^{-2} s^{-1}) by 90% during flowering and by 64% during pod development. Stomatal conductance was reduced up to 86% (in MNANJE) and up to 90% (in DodR). The highest percent decrease in transpiration rate (mmolH_20 m^{-2} s^{-1}) (88%) was revealed in NALBAM 4 and lowest in MNANJE (46%). Percentage change in relative water content ranged between 20% in MNANJE and 34% in NALBAM 4. The highest percentage decrease in chlorophyll content (10%) was recorded in DodR and the lowest (3%) in S19-3. Chlorophyll content in MNANJE increased by 11% and 6% as a result of insufficient water supply during flowering and pod development, respectively. This implies that, genotypes/species that can maintain appreciable leaf chlorophyll content during drought are able to sustain phostosynthesis and hence overall yield. The highest percentage decrease (26%) in rooting depth (cm) was observed in NALBAM 4 while MNANJE gave the minimum reduction (13%). MNANJE gave the highest root volume (46.64 cm^3) with lowest percent decrease (24%), while S19-3 gave percentage decrease in root volume of 49%. Water deficit stress also reduced the root surface area which ranged between 17% (S19-3) and 23% (NALBAM 4). Water deficit stress increased root length density in NALBAM 4 (by 82%) and DodR (by 73%). Lower percentage increase was observed in S19-3 (58%) and MNANJE (52%). During flowering stage, S19-3 had the highest percentage increase in root diameter (37%) while MNANJE gave the highest percentage increase in root:shoot (40%). Grain yield (t ha^{-1}) of both species significantly ($p < 0.001$) decreased with insufficient water supply. DodR was the most affected (65%), while the yield of MNANJE and S19-3 was reduced by 55% and 59% respectively. By maintaining appreciable amount of relative water content, early maturing, accumulation of high leaf proline content and deeper roots, S19-3 and MNANJE exhibit drought escape, avoidance and tolerance drought resistance mechanisms. The current

findings suggest that, MNANJE and S19-3 are drought resistant and can be grown in drought prone areas. The variations observed in the studied parameters among landrace-derived genotypes could be exploited in breeding drought resistance varieties for cultivation in drought-prone areas ultimately improving food security.

CHAPTER ONE

General Introduction

1.1 Background

Agriculture is an activity that is highly depending on climatic conditions for production of food and non-food commodities to sustain human life. Agriculture is vulnerable to climatic variability and change (USGCRP, 2014; IPCC, 2014; OECD, 2015; FAO, 2017a). The vulnerability of agriculture to climate variations is an issue of great importance to the global community (UNFCCC, 2006). Globally, impacts of climate change may seem to be negligible on total food production (Rosenzweig and Parry, 1994; Parry et al., 2004); however, some regions are expected to benefit from an altered climate, while other regions will be negatively affected (Battisti and Naylor, 2009; OECD, 2015; US-EPA, 2017). Most of the losses are expected to occur in lower-income countries in dry areas of Africa and Asia (Ali et al., 2017), whereas agriculture in the temperate areas where most of developed countries are, may benefit where technology is available and if proper adaptive adjustments are used (Ludi et al., 2007). For instance, by 2050, the farming yield production is expected to fall by 2.9% and 2.6 percent in West Africa and India respectively (FAO, 2018a), whereas yield in higher latitude regions like Canada and Russia harvest is expected to increase by 2.5% and 0.9% respectively (FAO, 2018a).

Changes in crop phenology (Marotzke and Forster, 2015) give important evidence of the response to current climate variations (Moa et al., 2017). Climate warming is expected to change plant growth and development, which is driven by environmental factors (Gray and Brady, 2016) and any amount of warming will lead to increased water deficit stress. In tropical

areas where agriculture depends mostly on rainfall, reports show that yields of some crops will be reduced because of minimal increases in temperature (IPCC, 2014).

Many people worldwide depend on rain-fed agriculture, which is vulnerable to effects of climate change. Global warming has increased frequencies of droughts and they are expected to have pronounced negative effects to African countries, countries in South Europe, Asia, Australia and America (Dai, 2011; Naumann et al., 2018). Their impacts are promoted by high water demand, increased population and shifting to urban areas (Mishra and Singh, 2011). Droughts negatively affect both crops and livestock (Ding et al., 2011). It is estimated that, 70 percent of the global population depends on farming, and 40 percent of all exports comes from agriculture (WRI, 1996). About half of the income in Africa is from agriculture whereby crop sector and livestock keeping account for about half of the household income (WRI, 1998). According to Davis et al. (2017), agriculture continues to be mainstay of smallholder farmers in Sub-Saharan Africa (SSA). Virtually all rural households (92%) have an on-farm activity (Davis et al., 2017). Africa has about 51 million farms of which 80% (or 41 million farms) are smaller than 2 ha in size (Lowder et al., 2016). Most of the poor and hungry people in the world are in rural areas who earn inadequate livings from agriculture (FAO, 2017b). The poorest members of society, in most low-income countries, are those who depend much on agriculture for income generation (FAO, 2014a).

Droughts are commonly classified by type as meteorological, agricultural, hydrological and socioeconomic (Wilhite and Glantz, 1985; WMO, 2006). Meteorological (weather-related) drought occurs when there is prolonged duration of less rainfall compared to usual rainfall pattern. It is region-specific and the causative of the other drought types (Chen et al., 2009). Hydrological drought occurs when there is insufficient rainfall to supply water to other water

sources like stream flow, reservoir and lake levels, and ground water table decline (https://www.weather.gov). Agricultural drought occurs when there is insufficient soil moisture, and rainfall is not enough to support crop growth to final stage causing crop stress and fall in yields (Wilhite and Glantz, 1985; Tekle and Alemu, 2016). Socio economic drought depends on the other three types of drought on availability, supply and demand of economic services and goods (https://www.weather.gov). Agricultural drought is more concerned with cultivated plants as opposed to natural vegetation. Agricultural drought can occur at the early, middle and later stages of crop growth (Martnez Fernndez et al., 2015; Vyas et al., 2015).

1.2 Rationale of the study

Climate change is already affecting agriculture production and food security (FAO, 2016c) and without urgent action millions more people will suffer hunger and poverty (FAO, 2018a). By 2050 number of people globally is expected to reach 10 billion (FAO, 2017b). The global world depends mainly on three cereal staple crops viz maize (*Zea mays* L.), wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) (Ray et al., 2013; OECD/FAO, 2018). Soybean is the fourth most important commodity crop (FAO, 2014b) after the major three cereals. Cereals contain small amounts of proteins and micronutrients providing on average about 9 g protein, 10 - 140 mg calcium, 0.5 mg iron and 0.6 to 3.3 mg zinc per 100 g serving (McKevith, 2004). This is much lower compared to grain legumes and hence validates the necessity to support grain legumes in complimenting diets from cereals. Combining the four, wheat, rice, maize, and soybean provide two-thirds (about 60%) of human caloric intake (Zhao et al., 2017). However, these crops are expected to be negatively affected by the climate change (Ringler et al., 2010). For instance, global increase in temperature by 1^{o}C is expected to reduce world production of different crops such as corn by 7.4%, wheat by 6.0%, rice by 3.2%, and soybean by 3.1% (Zhao

et al., 2017). Worse still, wheat is expected to disappear in Africa by 2080s (IPCC, 2007). With these effects of climate change, it is important to focus on different methods/approaches for safeguarding food as well as nutritional quality of food (Chivenge et al., 2015). Some suggestions have been made to make use of indigenous and underutilised species (Massawe et al., 2015; Mabhaudhi et al., 2016). Neglected and underutilized species (NUCS) are staple food crops that have normally slight monetary significance and not considered by plant breeding community (Naylor et al., 2004; Foyer et al., 2016). NUCS have been publicised as having resistance to numerous environmental traumas including drought (Mabhaudhi et al., 2016). According to Adeboye and Emmanbux (2017), such underutilized crops include grass pea (*Lathyrus sativus*), bambara groundnut (*Vigna subterranea* L. Verdc), cowpea (*Vigna unguiculata*) and marama bean (*Tylosema esculentum*). As opposed to cereal crops, legume crops are known for their ability to resist water deficit stress and high temperatures, while fixing atmospheric nitrogen (Osakabe et al., 2014). Underutilized legumes combat incursions of new diseases and pests, survive in hostile or deficient soil environments, have lower greenhouse gas emissions and contribute to Carbon sequestration in the soil (Herridge et al., 2008; Peoples et al., 2009; Massawe et al., 2016). In addition, these underutilized crops are considered as potential candidate crops against projected climate change and its consequences e. g food insecurity (Padulosi, 2009). Bambara groundnut is an important source of dietary protein (16-25%), carbohydrates (55-72%) and oil content (6-7%) (Suwanprasert et al., 2006); Fat (4.5%-7.4%), Fiber (5.2%-6.4%), (Ash 3.2%-4.4%) and Minerals (2%) (Murevanhema and Jideani, 2013). The high nutritional qualities of bambara groundnut made it a complete food (Bamishaiye et al., 2011) and hence an ideal candidate for food security in the changing climate (Chivenge et al., 2015; Cleasby et al., 2016).

Mabhaudhi et al. (2018) used the AquaCrop model to investigate the outcomes of variations in climate on bambara groundnut production, water consumption and output from used water (water productivity). The author used data of past period (1961 to 1991), current (1995 to 2025), mid-century (2030 to 2060) and late century (2065 to 2095). Simulations projected that, yield as well as output from water consumed (water productivity) by bambara groundnut will raise by 37.5% and 33%, respectively, between 2065 - 2095 (Mabhaudhi et al., 2018). However, there is limited scientific data on how bambara groundnut responds to drought with respect to metabolic processes, phenology, yield, resource capture and conversion (Mwale et al., 2007a). Landrace variations following insufficient water supply has been reported (Collinson et al., 1996; Aliyu and Massawe, 2013; Molosiwa et al., 2015). Yet, causal traits and mechanisms have not been sufficiently established (Mwale et al., 2007a). Moreover, although physiological studies have shown the function(s) of some traits, e.g. rooting depth and photosynthate remobilization, their mechanisms have not been studied in detail (Begemann, 1988; Muhammad and Massawe, 2015).

Lack of improved drought resistant bambara groundnut varieties (Mabhaudhi and Modi, 2011) and their characterization, remains a challenge to increasing yields of bambara groundnut. Identification and promotion of resistant bambara groundnut landraces/genotypes/varieties is of great importance. According to Shiferaw et al. (2014), integrated strategies that combine agricultural technologies for drought mitigation include use of drought resistant crops and varieties to reduce drought risk in drought prone areas. To achieve development of water deficit stress resistant and high yielding varieties, understanding of the effect of water deficit stress cannot be disregarded. For the prevailing climatic change and their expected threats, it is now high time to make use of the unexploited potential in

legumes, especially bambara groundnut. Understanding the mechanisms involved in drought adaptation, will provide important facts for plant breeding stakeholders on suitable parameters as well as strategies against drought (Cullis and Kunert, 2017). Therefore, studying bambara groundnut and groundnut for adaptation to drought will later directly and indirectly mitigate the expected food and nutritional insecurity. It is without doubt that, plant breeders will easily be able to target the desired traits for crop improvement and farmers will have a choice to grow crops according to their performance in a certain area rather than growing them as a routine.

1.3 Overall hypothesis

The imposition of water deficit stress will cause negative effects on growth and development, yield components and yield of both bambara groundnut and groundnut. It is also thought that, bambara groundnut is more drought resistant than groundnut.

1.4 Aims and Objectives

1.4.1 Aims

The project explores the mechanisms associated with drought resistance in bambara groundnut and groundnut. The project also aims to provide a comparison on the degree of drought resistance between bambara groundnut and groundnut.

1.4.2 Specific Objectives

i. To assess the effect of soil water deficit stress on yield components and yield of bambara groundnut landraces and a groundnut variety.

ii. To determine the effect of soil water deficit stress on chlorophyll, stomatal conductance, relative leaf water content and growth parameters.

iii. To determine the effect of soil water deficit stress on the biochemical trait, proline accumulation in the leaves.

iv. To determine the effect of soil water deficit stress on root traits of bambara groundnut and groundnut.

v. To compare the drought response of selected bambara groundnut landrace-derived genotypes with that of a groundnut, MNANJE, grown under similar conditions.

1.5 Structure of the Thesis

The thesis is comprised of seven chapters. Chapter One, the current chapter, gives a general introduction of the research study, its justifications, aims, objectives, general hypothesis and a summary of the structure of the thesis. Chapter Two reviews the literature on water and its role in crop production. Drought and its importance to plant systems and how plants sense and respond to it is also reviewed. The chapter also reviews the literature on bambara groundnut and groundnut, including their origin, production and drought resistant potential. Chapter Three narrates the general methodology employed in the current research. This includes materials and methods that generally apply to the various experiments carried out in the research work. Materials and methods more particular to some experiments are further described in specific sections in the chapters where the experiments are presented. Chapters Four, Five and Six present the details of the experiments carried out to assess the response of bambara groundnut and groundnut to water deficit stress. Each of the chapters presents the details of the particular experiment(s) in the chapter and is made up of sections describing the relevant methodology, results and discussions. Chapter Seven summarises and gives a

general discussion of the results of the research work. Chapter Seven ends with concluding remarks from the research work.

CHAPTER TWO

Literature Review

2.1 Introduction

Agriculture is the superior form of land use worldwide involving major social, economic, and cultural activities which provide various services to people (Shiferaw, 2014). However, agriculture is very sensitive to climate variations. Most of smallholder farmers in sub-Saharan Africa (SSA) depend on rain fed agriculture for their livelihoods, and they are often affected by variability in climate change (Gautam, 2006). Changes in rainfall has a large negative effects on the livelihoods of the poor and the economies of most of the African countries (Gautam, 2006; Hellmuth et al., 2007). Agriculture is the main source of national income for most developing countries (FAO, 2004; Doungmanee, 2016). Agriculture and climate change are interrelated and are both global issues influencing food security. The impact of climate change is unevenly distributed all over the world (Battisti and Naylor, 2009). In some areas temperature and rainfall will increase; while in other places rainfall is expected to decrease (Schneider, 1989). The effects of climate change on crops are expected to be negative in tropical areas whereas in temperate areas, the effects are expected to be negative or positive (Battisti and Naylor, 2009; FAO, 2018b). Areas of South Asia and SSA with high population, are more vulnerable to climate change (Wheeler and von Braun, 2013; AGRA, 2014; Chattaraj et al., 2014). The SSA region is predicted to suffer crop yield losses of at least 20% by 2050 with 40% and 30% risks of crop failure for corn and wheat, respectively (Adhikari et al., 2015). Risk of food insecurity is expected to be increased by climate change for some vulnerable community groups (Cline, 2008). Climate change affects agriculture through changes in temperature, rainfall and variations in atmospheric CO_2 and alterations in the dietary value of

certain food stuffs (Hoffmann, 2013). A report by USDA (2009) indicated that increased carbon dioxide levels might accelerate the growth of some crops. Though rising carbon dioxide can stimulate plant growth (IPCC, 2013), CO_2 also reduces the nutritional quality of many crops (Loladze, 2014). Increasing levels of atmospheric CO_2 reduce the concentrations of protein and essential minerals in most crops, e.g. rice, wheat, and soybeans (USGCRP, 2014; Smith et al., 2017; Zhu et al., 2018). Shifts in food production are expected as a result of global climate change (Rosenzweig and Iglesias, 1993; FAO, 2017c). For instance, in Benin, reduced rainfall and increased rainfall variability is projected to reduce production of maize and yam (Sonneveld et al., 2011), in Niger, millet production is expected to decrease between 11% to 26% by 2025 (Mohamed et al., 2002) and in Tanzania climate change is likely to promote rice diseases leading to reduction in yield (Doku et al., 2016).

Both of these factors, climate change and agriculture, interact. Agriculture uses about 70 percent of all freshwater (Molden, 2007). The water from aquifers is mostly drawn for agriculture uses (FAO, 2011a), and the rate at which agriculture draws water from the underground water sources is unsustainable (Castle et al., 2014). Underground water sources in areas of China, United States and the Upper Ganges are in a risk of depletion (Li, 2012). Water used for agriculture is associated with environmental troubles, such as the wetlands destruction, the blowout of water-related diseases, and land/soil degradation (build up harmful salts and poor soil aeration) (FAO, 2005). Agriculture is known to contribute to variations in global climate through elevated greenhouse gases as well as deforestation (turning forests to agricultural land) (HLPE, 2012). The contribution of changes in agricultural practices ranged between 20 - 25% to worldwide total greenhouse gases (GHGs) in 2010 (Hoffmann, 2013). Thus, agriculture becomes a driver of changing climatic conditions. Apart

from agriculture, industrial development and increased urbanization, increase the demand for water; meaning lack of enough water is growing and crop farming is under pressure of increasing food production to feed global population growth (FAO, 2013a). Human population is projected to be more than 9.3 billion by 2050 (USCB, 2014). Plant foods are known to exert lower environmental effects compared to animal food products (Masset et al., 2014), and health of vegetarians and vegans appears to be better than that of non-vegetarians (Appleby and Key, 2016). A study on diet preferences revealed a shifting from animal foods to plant foods for various reasons (Pergnon et al., 2017). Increased shifts in diets toward plant foods will obviously put more pressure on crop production. It is expected that, by 2050, much of the world will experience regular higher temperatures than the hottest now and this will possibly go together with fluctuations in rainfall pattern (Battisti and Naylor, 2009; FAO, 2018b).

Research and predictions using models show the possibility of yield reduction of 6 to 10% per one degree Celsius increase in the mean temperature during cropping period (Guarino and Lobell, 2011). This implies that significant production losses are expected in the coming years. Opening more land for increased food is not a sustainable choice in most areas of the world without paying attention to sustainable alternatives (Garnett et al., 2013). It is worthwhile to focus on improving crop cultivars that will cope with the changing abiotic factors (Hannes et al., 2014) and adopting crops, (like underutilized legumes), that are resistant to harsh environments.

Legume crops possess potential characteristics against climate change threats. Legumes have ability to resist drought because of their interaction with Nitrogen-fixing bacteria and arbuscular mycorrhiza (Lodeiro et al., 2000). Furthermore, legumes survive under various climatic conditions as well as on different soil types (Daryanto et al., 2015). Legumes are

known to have developed various mechanisms (from cellular level to whole plant) which make them to endure under harsh growth situations (Osakabe et al., 2014; Tatrai et al., 2016). This calls for the need of exploiting legumes hidden and unutilized treasure in a breeding perspective. Over the past 50 years, efforts on crop improvement have been directed to cereals (Pingali, 2012). Improving the current breeders' techniques, give an opportunity to increase the rate of crop genetic improvement (Phillips, 2010). Attempts to exploit new molecular tools, especially the ability to study in detail the genetics of quantitative traits e.g. yield and various stress resistance (Tuberosa, 2012; Cobb, 2013) are limited by ability to carry out phenotyping. Apart from the ability to phenotype, phenotyping attempts are limited in legumes, with very few attempts applied to specific legume crops (Monneveux, 2014). For example, to date no literature or documented material showing phenotyping for drought in bambara groundnut. Currently, efforts to improve high-throughput platforms for field phenotyping remain a challenge in breeding community (Araus and Cairns, 2014).

Therefore, there is a need for further investigation of drought-related phenotypic traits and their associated mechanisms against water deficit stress in bambara groundnut and related species. Subsequently, contributing to efforts in improving food security especially among the vulnerable groups in the drought prone areas.

2.2 Soil moisture and drought

Lack of enough irrigation water/rainfall (drought), causes insufficient soil moisture followed by reduced plant tissue water. Drought stress is harmful to crop production as it reduces yields, which leads to reduced food availability and hence increased food demand and prices (Matoboa et al., 2017). The lack of enough water (water deficit) or excess water (water logging) in the environment causes water stress and then injury to plants (Sairam et al., 2008).

Water stress in the plant affects many plant's metabolism, resulting to stunted growth and reduced yield. When crops in the field are exposed to unsuitable conditions crop yields can be reduced. Boyer (1982) reported separate yield reduction (69%) of wheat and maize in North America due to heat and water scarcity. Drought itself reduced wheat production in Diyarbakır Turkey by 61% in 1999/2000 cropping season (Kilic and Yagbasanlar, 2010). FAO (2017a) reported on average (2005 -2014) 19% crop losses due to drought. Under insufficient water, plant water relations experience three main development stages (Blum, 1997). In stage one, both water loss (transpiration) and CO_2 absorption (assimilation) remain normal till the available soil water is reduced to a point where transpirational demand cannot be covered by water uptake. In stage two, water loss and CO_2 absorption declines below the threshold level. Following decrease in soil moisture, insufficient water in plants increases. The last stage, stage three, occurs when the stomata are completely closed and water loss from plant is not primarily from stomata. The time that the plant can withstand stage three is species specific (Blum, 1997).

Soil type determines the amount of soil water content. A saturated coarse sand, holds far less water as compared to saturated heavy silty clay. This comes about because of distribution of soil particles in a given soil type. Sandy soil has large particles and also sand particles do not bind water. It is from these grounds that, sand soil has a much lower water content compared to clay soil. The amount of water available to a crop in the soil is controlled by two factors viz concentration of soil moisture and the soil volume reached by plant roots. Water uptake and water transpired need to balance in order to avoid water deficit in the plant tissue (Shamudzarira, 1996). Insufficient water in the soil affects most of the plant processes from

cellular to whole plant. Water deficit stress restricts vegetative growth of bambara groundnut, which led to reduced total dry matter (see Mwale et al., 2007a).

2.3 Response of soil health to changing climate

Soil health or soil quality, is defined as the continued capacity of soil to function as a vital living ecosystem that sustains plants, animals, and humans (https://www.nrcs.usda.gov). Climate change has a potential influence on the soil health through physical, chemical and biological properties of soil (Patil and Lamnganbi, 2018). Together with soil organic matter, soil pH, cation exchange capacity (CEC), microbes are very important in ensuring the good soil quality.

Soil pH depends very much on climate. It is considered as an important indicator of soil health. Soil pH has thus been included in integrative soil health tests to assess impacts of land use change and agricultural practices (Nanganoa et al., 2019). Most soils would not be subjected to rapid pH changes resulting from drivers of climate change such as elevated temperatures, increased atmospheric CO_2, variable rainfall and atmospheric N deposition. Nevertheless, these drivers of climate change will negatively affect soil microbes, soil organic matter, soil nutrients, CEC, plant available water; which in turn will affect soil pH and hence plant productivity (Patil and Lamnganbi, 2018). Soil organic matter accumulates when microbial decomposition occurs at rates lower than additions of organic matter. Study by Nanganoa et al. (2019) revealed negative significant correlations between pH and number of earthworms and between ants and bulk density (a function of soil organic matter).

In order to make sure that soil health is maintained for sustainable crop productivity against negative effects of climate change, efforts are under way to find the solution. Bonfante et al. (2019) have proposed a way forward. The authors suggested that, instead of dealing with physical, chemical and biological aspects of soil health separately, a combined approach would be more appropriate. Starting with pedological and physical aspects followed by chemical and biological all together, would maintain the good soil quality.

2.4 Plant growth, drought, climate change and yield

Plant growth and development depends on interactions involving source and sink limitations of the main structures of a plant, the root system and the shoot, creating useful balance (Shakeel et al., 2011). Any of water deficit stress (permanent or temporary) adversely affects the plants' performance compared to any other abiotic stress (Shakeel et al., 2011). Different plant parameters has been used to measure/assess its growth. These include; leaf area, plant height, shoot biomass, root biomass and total plant mass (Fageria et al., 2006). Limited water supply is the major environmental stress hindering improved crop yields (Chaves et al., 2003).

Poor seed germination and plant establishment are early effects of insufficient water supply (Harris et al., 2002). The growth of a cell is highly affected by drought as the result of decrease in turgor pressure. Growth is a function of cell production, division and expansion of the tender cells. Severe limited water supply disturbs water flow via xylem to plant cells and hence reduced total cells' growth and development (Nonami, 1998). Insufficient water supply negatively affects mitosis; cell growth and development leading to declined overall plant performance (growth and yield) (Hussain et al., 2008). Drought-promoted decrease in leaf area reduces development of the entire leaf caused by low rate of photosynthesis (Rucker et al., 1995). Decrease in leaf growth is considered as an adaptive response and it limits increase leaf area and eventually plant's transpiration rate (Lu and Neumann, 1998). As a consequence of reduced transpiration, ability of plant to survival may be prolonged by the period of availability of soil water content (Passioura et al., 1993). Reduction in photosynthesis under water deficit stressed leaves may be contributed by stomatal closure (Vurayai et al., 2011a, b) or non-stomatal factors. Higher stomatal conductance is positively correlated with photosynthesis. Higher photosynthetic rates contribute to higher biomass as well as final crop

yields. Reduction in plant biomass production is a common negative effect of water deficit stress in plants (Zhao et al., 2006). Water deficit stress significantly reduced stem length in different crops. For instance, Specht et al. (2001); Zhang et al. (2004) in soybean, Heuer and Nadler (1995) in potato (*Solanum tuberosum*), Sankar et al. (2007) in okra (*Abelmoschus esculentus*) and Petropoulos et al. (2008) in parsley (*Petroselinum crispum*).

Climate change and its impact on human-environment are immeasurable because of its massive negative effects. However, the effect is not same for all countries, it depends on the countries geographical settings. Because of climate change temperature is gradually rising, frequency of floods, salinity intrusion, and the volatility of rainfall has increased comparing to past (Sazedur and Ashfikur, 2019). All these led to the probability of decreasing the crop productivity. It is obvious that adaptation is an important part of reducing the negative effects of climate change (Quan et al., 2019) and subsequently sustaining farmers' livelihoods, ensuring agricultural sustainable development and food security. Some crops are known to survive under dry areas. Bambara groundnut (Mabhaudhi et al., 2018; Fieldman et al., 2019) and groundnut (de Lima Pereira et al., 2016) are adapted to arid and semi-arid areas and hence very important crops in this regard.

Most of processes contributing to plant yield are affected by limited water supply. Crop harvest (yield) combines numerous processes in a complicated manner. For instance, drought decreases crop output by preventing normal growth as well as photosynthesis rate (Taiz and Zieger, 1998). Crop photosynthesis rate and crop yield are positively correlated (Liang et al., 2017), however, changes in assimilate partitioning and utilization can result to reduction in the said correlation (Guo et al., 2002). Changes of growth patterns in plants plays a role to survive under water deficit environments. Among other changes in growth patterns associated with drought, is increased root: shoot proportion (Sharp et al., 2004; Yamaguchi

and Sharp, 2010). It is therefore difficult to interpret how plants accumulate, combine and display complicated processes through the plants life cycle. Many plant growth components associate and express themselves as grain yield. Water deficit results to severe decline in yield components of crop plants probably due to disruption of leaf gas exchange properties which not only limits the size of the source and sink tissues but also the phloem loading, assimilate translocation and dry matter partitioning (Farooq et al., 2009). Drought stress limits the biomass production because of its inhibitory effects on leaf expansion, leaf development which results to decrease in light interception (Nam et al., 1998). Flowering stage is very sensitive to drought. Decrease in assimilate flux to the evolving seed is the major cause of the drought sensitivity during flowering, though not the only one e.g. in pearl millet (*Pennisetum glaucum* (L.)) (Yadav et al., 2004). Low soil moisture retards general crop progress, and hence fewer flowers, fewer grains and poor grain filling. Poor grain filling is associated with reduced assimilate distribution and functions of starch and sucrose enzymes. Yield components of maize crop were reduced following supply of insufficient water during flowering (e.g. cob kernel rows, 100-kernel weight, and harvest index) (Anjum et al., 2011). The reductions caused by drought in plants might be due to reduced/closed stomata aperture as a reaction against insufficient moisture in the soil, resulting to reduced CO_2 absorption and transpiration (Cornic, 2000; Flexas et al., 2004).

Plant responses to insufficient water supply are complex, differing among species from point of the soil water acquisition and transport to other plant parts, rather than to extreme variations in metabolism at a given water level (Mabhaudhi and Modi, 2011, 2013). Carbon absorption at the entire plant level continuously declines because of restrictions to CO_2 circulation into the leaf, alteration of carbon allocation to non-photosynthetic structures and

defence molecules, or fluctuations in leaf biochemistry and therefore reduction in photosynthesis (Haworth et al., 2016). For instance, acclamatory variations in the ratio between root and shoot or the provisional assimilate build-up in the stalk of rice under insufficient water supply are escorted by changes in carbon and nitrogen absorption (Sikuku et al., 2010a). The acceptable regulation of this is still unidentified (Pinheiro et al., 2001). Drought resistant genotypes/varieties have deep and thick roots. The thick roots are positively associated with xylem vessel area, which are important to the movement of soil moisture to the above ground parts (shoots) to compensate amount of water lost by transpiration (Pinheiro et al., 2001; Nardini et al., 2011; Chavarria et al., 2012).

2.5 Mechanisms of adaptation to drought

The terms *drought tolerant* (DT) and *drought resistant* (DR) are often used interchangeably—and incorrectly so. Drought resistant plants, drought tolerant plants, drought adapted plants, low -water- use plants, are all terms used to describe whatever plant is thought to be drought tolerant. *'Drought tolerance'* refers to capability of plants to resist inadequate water in plant tissues via adaptive traits (Morgan, 1984). These adaptive traits include upkeep of cell turgor through osmotic modification and cellular elasticity, and raising protoplasmic resistance (Morgan, 1984). DT species are true desert plants (https://tjsgardendotcom). A plant that has certainly grew to endure times of drought with water scarcity and has the capability to withstand substantial desiccation of their tissues and structures is drought tolerant (e.g. xerophytes). For instance C4 Carbon Fixation or crassulacean acid metabolism (CAM) are carbon fixation conduit that developed in some plants as an adaptation to arid environments. In a plant utilizing full CAM, the stomata apertures close during the day and open at night to accumulate carbon dioxide. The carbon dioxide is kept and then used in photosynthesis.

'Drought resistance' is a wider term applied to plants with adaptive structures that allow them to escape, avoid, or resist drought stress (Levitt, 1980). DR plants are not exact desert plants. Many of DR plants have originated in semi-arid regions, the area nearby the Mediterranean, Latin America and sub-Sahara Africa (https://tjsgardendotcom).

It can be viewed that, drought tolerant plants are those with the ability to limit the harm or damage caused by water deficit, whereas resistant plants are the ones that are only able to limit the stress itself but not the harm/damage caused by the stress. In this context therefore, the term drought resistance will be used when referring to crops ability to limit water deficit stress.

Adaptation to drought includes a variety of mechanisms that allow plants to persist and yield in times of dry conditions. The strategies against drought are clustered into three groups viz escape, avoidance and tolerance (Levitt, 1980; Blum, 2005). A plant's specific mechanism for surviving under stress depends on the nature of the reactions it assumes in countering the emerging water deficit stress. Gowda et al. (2011), highlighted four forms of drought-resistance associated mechanisms in plants: (i) *drought avoidance*, e.g. getting water from the soil using deeper roots, (ii) *drought escape*, this occurs when the flowering time avoids the water scarcity period, (iii) *drought resistance*, this involves maintenance of the intracellular water potential and (iv) *drought recovery*, growth regaining after water deficit stress period.

Drought escape occurs when a crop matures before the progress of severe limited soil and crop moisture. This includes early maturation to avoid severe terminal water deficit stress (Berger et al., 2010). It is mainly associated with quick phenological progress, developmental plasticity (difference in duration of growth time depending on the degree of water shortage),

and remobilization of photosynthates to the grain. According to Araus et al. (2002), flowering is a key adaptation allied to drought escape. They further stated that escape arises when crop phenology, such as time to flowering, is closely synchronised with times of water accessibility, mainly when the growing period is characterized by terminal drought (Farooq et al., 2009).

Drought avoidance occurs when the crop is able to keep relatively high water level in the tissue, irrespective of scarcity of moisture in the soil (Levitt, 1980). This approach comprises reserving water in the tissues during relatively short periods of critical stress during the crop growth and development to avoid permanent injury (Berger et al., 2010). The importance of drought avoidance is to decrease loss of water while improving or keeping uptake by the plant roots. Drought avoidance includes crop reactions like stomatal regulation, improved soil water capture by extensive and high-volume root system (Turner et al., 2001; Kavar et al., 2007). Numerous root features such as length, depth, biomass and thickness (volume) are believed to contribute to final yield under water deficit situations (Subbarao et al., 1995; Turner et al., 2001; Kavar et al., 2007) due to improved water capture. In addition, drought avoidance is achieved by decrease of water loss through declined stomatal conductance, reduced heat absorption via leaf orientation, and reduced leaf surface evaporation.

Drought tolerance or *plant survival to drought* has been described as the ability of a plant to sustain metabolism in water deficit stress conditions (Blum, 2005). Berger et al. (2010) described this strategy as “overall resistance to drought”. It is vital as most of the crop growth and development operates under water scarcity conditions, so plants need to keep their general growth and metabolism. It is accomplished through upkeep of turgor through osmotic adjustment (accumulation of metabolites, osmoprotection e.g. proline) and the antioxidant resistance systems (Farooq et al., 2009). Blum (2005) provided a thorough explanation of

increasing proof telling a connection among great osmotic modification and maintenance of plant biomass and yield in stress conditions. He showed that, an operational drought resistant mechanism in crop plants is stem backup exploitation for grain filling under insufficient water supply.

Figure 2.5.1 as taken from Berger et al. (2010) summarizes the drought resistance mechanisms. Each box designates at which stage specific plant strategies could be beneficial to cope with water deficit.

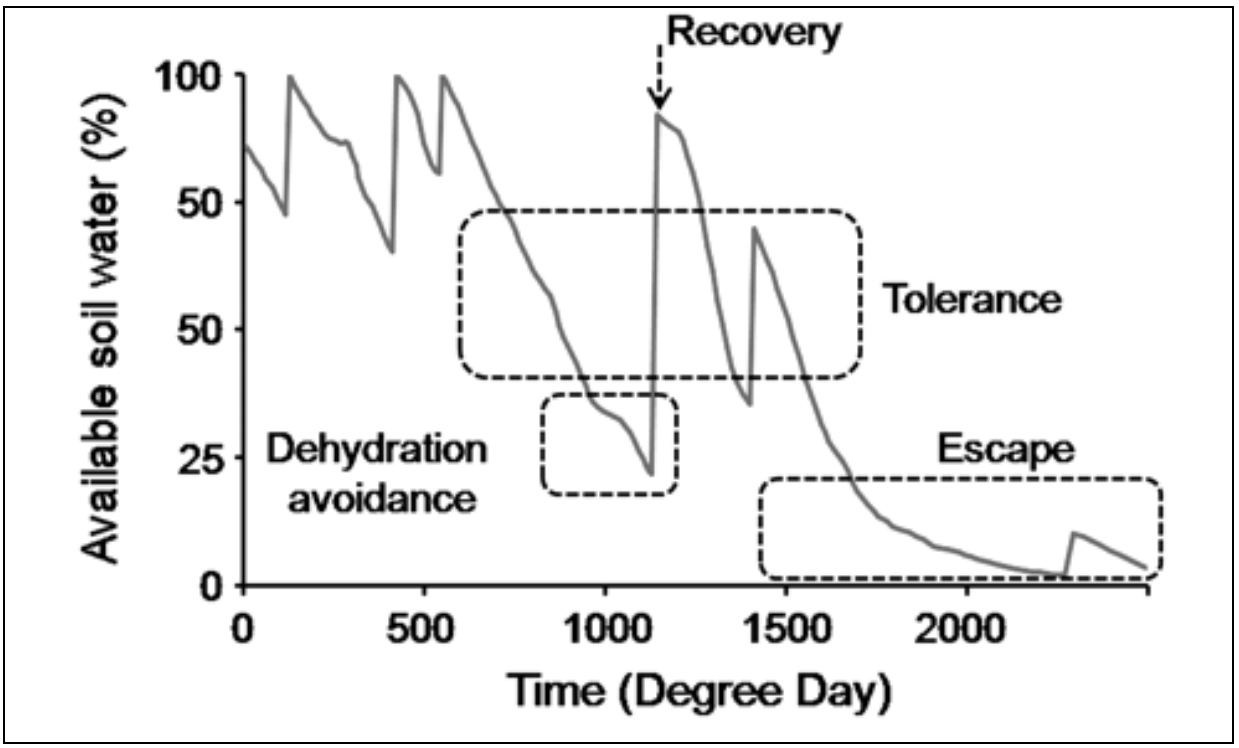


Figure 2.5.1: Soil water accessibility during a wheat crop cycle at Roseworthy in 2007 season.

2.6 Water Use Efficiency (WUE)

Water-use efficiency (WUE) is described as the ratio of water utilized in plant metabolic activities to water lost via transpiration. Commonly referred types of WUE are photosynthetic also known as intrinsic or instantaneous WUE and productivity WUE. Photosynthetic WUE is the ratio of the rate of photosynthesis (carbon absorption) to the rate of transpiration. It

offers a direct measure of activity of the photosynthetic system standardised to constant gaseous and water movement in and outside of a leaf (Bacon, 2004). Traits that tend to keep water (conservative traits) have low stomatal conductance, low leaf growth rate, or deep root systems offer improved water use efficiency (Bacon, 2004). Although researchers often tend to employ instantaneous/intrinsic WUE values as a physiological marker for drought resistance, other means of measuring WUE exists. The other type is productivity water use efficiency (PWUE), also referred to as integrated WUE. This type takes consideration of whole plant over the growth season. Connor et al. (1992); Chaves and Oliveira (2004) describe this type of WUE as the ratio of production of biomass, shoot biomass or harvested yield to water supply or total evapo-transpiration or plant transpiration. Regardless of the method used to measure WUE, higher values indicate drought resistance and vice versa is true. Plant materials with higher WUE values can assimilate carbon at low stomatal conductance and later achieve a better yield by using less water (Johnson et al., 2018). Enhanced water-use efficiency is usually known as a reaction mechanism of plants to mitigate serious soil water deficits, e.g. in bambara groundnut (Mabhaudhi et al., 2013) and in groundnut (Songsri et al., 2013). Furthermore, it has been the attention of numerous researchers to increase crop resistance against water scarcity. Nevertheless, there is some question as to the advantage of improved water-use efficiency of plants in agriculture, as the processes of enhanced yield production and reduced transpirational water loss (the main driver which increases in water-use efficiency) are basically contrasting (Bacon, 2004). Water spenders attain higher tissue water level by preserving the water uptake through improved rooting and hydraulic conductance under insufficient water conditions. On the other hand, water savers use water efficiently through condensed loss of water by decreasing transpiration, transpiration area and heat absorption in drought stress at the expense of final yield. If there was a situation where water

shortage induced lower transpirational rates without concurrently declining photosynthetic rates and plant biomass production, then water-use efficiency would be both importantly enhanced and a preferred trait in crop production (Tambussi et al., 2007; Lambers et al., 2008). According to Nageswara Rao et al. (1985); Arunyanark et al. (2008) drought stress significantly reduced WUE in groundnut.

2.7 Crop phenology

Phenology is the study of seasonal events in the life cycles of plants or animals, as influenced by the environment; especially seasonal variation in temperature and precipitation (Cleland et al., 2007). Shifts in phenology, productivity, distribution and biodiversity of individual species depend very much on climate change (Wolkovich et al., 2012; Schröder et al., 2014). Plant phenology is the timing of plant life cycle events, such as bud/bloom appearance, flowering, fruiting/pod formation, pod filling (Stuck et al., 2018). According to Leith (1974), phenology is the developmental timing in relation to the calendar. Phenological studies of crop growth are important to mitigate the negative effects of climatic variations (Yasmin and Nehvi, 2018). Singh (2003), outlined three major phenophases in groundnut viz expansion, podding and filling. On the other hand, Williams et al. (1978), divided the groundnut life time into ten phases namely; *Stage 1:* germination and emergence; *Stage 2*: vegetative growth only; *Stage 3:* vegetative growth and first flowers; *Stage 4:* active flowering with first pods being produced; *Stage 5:* flowering, peg production, pod production and the start of significant kernel growth; *Stage 6:* vegetative growth ceasing and rapid kernel growth commencing; *Stage 7:* pod initiation ceasing and rapid kernel growth continuing, defoliation usually starts; *Stage 8:* first mature pods present; *Stage 9:* 30 to 40% of the pods mature; *Stage 10:* 50 to70% of the pod mature, defoliation rapid and crop lifted at the end of this

phase. Boote (1982) divided the phenology of groundnut into vegetative stages and reproductive stages. *Vegetative stages* (VE = emergence, V0 = cotyledons are flat on the soil and V1 – Vn = first tetrafoliate to n^{th} tetrafoliate). *Reproductive stages* (R1, R2, R3, R4, R5, R6, R7, R8 and R9 representing beginning bloom, beginning peg, beginning pod, full pod, beginning seed, full seed, beginning maturity, harvest maturity and over-mature pod respectively). Phenological stages of bambara groundnut have been divided into five stages which are emergence, vegetative, flowering, pod filling and maturity (Karunaratne et al., 2010).

According to Wopereis et al. (1996), insufficient soil moisture at any stage will affect plant growth. Bambara groundnut has been found to flower earlier in water deficit conditions (Mabhaudhi and Modi, 2013) and is more affected during flowering than during pod filling (Vurayai et al., 2011b). Insufficient water supply during any period of plant development, has been linked to yield and total dry matter reduction (Mwale et al., 2007a; Karunaratne et al., 2010; Vurayai et al., 2011b).

2.8 Drought resistance in grain legumes

Legumes are grown in almost every climatic region and on a varied range of soils (Daryanto et al., 2015). Legumes are second to cereals in terms of contribution to food security (Akibode and Maredia 2011). Legumes are exceptional in their ability to resist drought for their interaction with Nitrogen-fixing (i.e., rhizobia) bacteria and arbuscular mycorrhiza (Frechilla et al., 2000; Lodeiro et al., 2000). Legumes are generally resistant to drought but there are known variations among species and varieties (Daryanto et al., 2015). Most of legumes are major cash crops for many smallholders in developing countries. The total world export of six major crops is estimated to be more than US$21.8 billion; soybean contributing 83.8%,

common bean (8.8%), groundnut (4.9%) and chickpea (2.4%) (Abate et al., 2012). In the previous 50 years, worldwide cereal production has almost increased thrice whereas legume production has only raised by about 60%, soybean being the main contributor (Foyer et al., 2016). Grain legumes has shown low rate of yield increment relative to cereal crops; this can be explained in part by the low genetic diversity in grain legume improvement programmes (Cowling et al., 2017). Legumes are also presently underutilized (Nah and Chau, 2010) relative to cereals in systems of crop cultivation, although the benefits of intercropping and rotation of grain legumes with cereals or other crops are well known (Peoples et al., 2009; Araújo et al., 2014). Such benefits include improved crop yield, improved nitrogen-use efficiency, and reduced incidence of plant diseases and pests. Intercropping with grain legumes is now seen as an important mechanism for vertical intensification (value addition in the yield from different crops), as well as enabling rise in biodiversity and generating a more varied landscape for animals and insects (Jensen et al., 2010). A main task in the future will be the selection of legume species and cultivars, which could be successfully introduced across various cropping systems (Stagnari et al., 2017).

Bambara groundnut and groundnut although from different species, have more or less similar characteristics. Both legumes bear seeds underground and fix atmospheric nitrogen through nodulation (de Faria et al., 1989). They are commonly grown as rotational crops with legumes like cowpea (*Vigna unguiculata*) and cereals like maize (*Zea mays*), sorghum (*Sorghum bicolor*) and millet (*Pennisetum glaucum*) in agroecological regions that receive minimal annual rainfall (Hillocks et al., 2012). Furthermore, they both play the central roles of human food and animal feed security (Voisin et al., 2014), crop intensification, diversification and mitigation of greenhouse gases emissions (Peoples et al., 2009; Jensen et al., 2010). With these valuable

attributes offered by these two important legumes it is worthwhile to fully utilize them to as a precaution to effects of climate change.

2.9 Bambara groundnut

2.9.1 Origin and History

Bambara groundnut or bambara nut (*Vigna subterranea* (L) Verdc), synonym (*Voindzea substerranea* (L.) thours), belongs to the family Fabaceae and sub family Faboidea (Bamshaiye et al., 2011). The name bambara originates from bambara district, near Timbuctoo. It is also known as 'njugu mawe' in Tanzania (Hillocks et al., 2012), 'jugo beans', 'izindlubu', round beans in South Africa (Swanevelder, 1998) and 'nyimo' in Zimbabwe (Mungate, 1995). Bambara groundnut is a leguminous crop native to Africa and cultivated with minimal inputs by small holder growers in dry environments (Basu et al., 2007b; Massawe et al., 2002; 2007). It is a common pulse grown mostly by subsistence women farmers in drier areas (Goli, 1995).

2.9.2 Botany, ecology and production

Bambara groundnut is a low flat annual with compound leaves made of three elliptic leaflets (Stephens, 2012). The leaves are on long petioles that originates from short stems just above ground level (*Figure 2.9.1*). The cultivated forms of bambara groundnut have stems with a limited creeping growth habit, which gives rise to either bunch or intermediate types (Linnemann and Azam-Ali, 1993). The morphology of bambara groundnut is similar to that of groundnut (*Arachis hypogaea*).

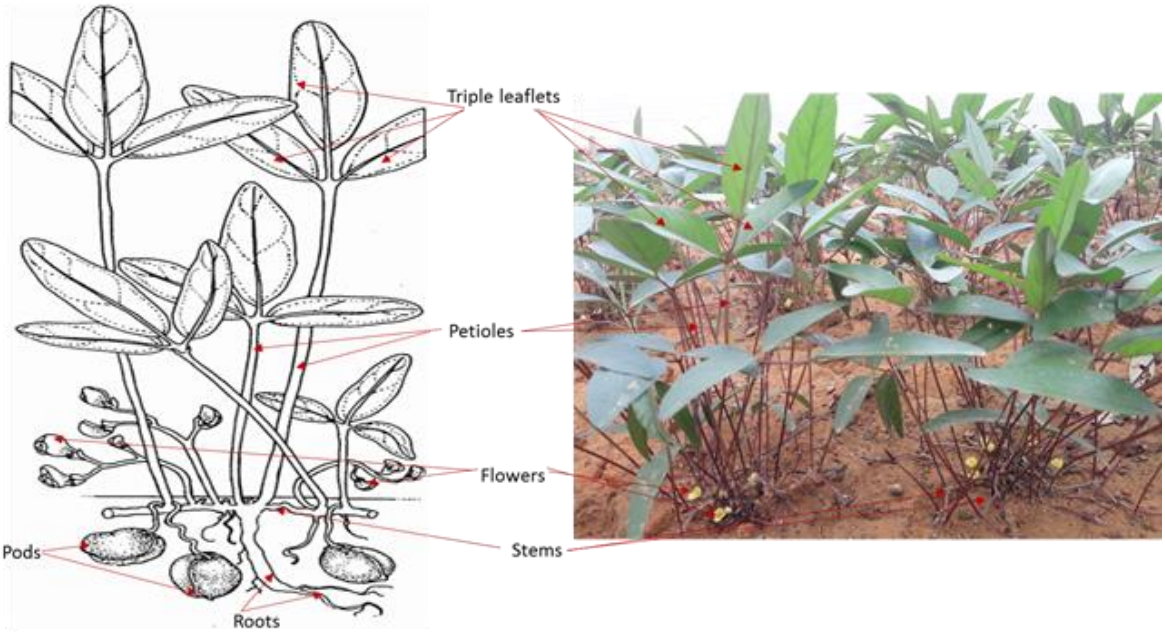


Figure 2.9.1: Morphological features of bambara groundnut (Vigna subterranea L. Verdc).

Yellow or cream in colour flowers are formed on short racemes near the ground (*Figure 2.9.2*). Pods have one or two seeds formed below the ground. Bambara groundnut is grown from true seed together with crops like corn, millet, sorghum, cassava, yam, peanut, and cowpea (Gibbon and Pain, 1985; Karikari et al., 1997; Ocran et al., 1998). Tindall (1997) showed that shelled seeds are sown on beds/ridges spaced at 40 cm - 50 cm and plants spaced at 20 cm - 30 cm within rows.

Figure 2.9.2: Bambara groundnut showing: leaves and leaflets (left), flowers (middle) and pods (right).

According to Ocran et al. (1998), the recommended plant spacing is 10 to 45 cm (between rows) by 15 to 17 cm (between plants). Sowing depth of 3 to 5 cm is usually used with one

seed per hole. Seed rate varies from one location to another. For instance, 35 kg ha^{-1} in Tanzania; 25-45 kg ha^{-1} in Kenya; seed rate of 60-75 kg ha^{-1} has been used in South Africa in order to compensate rat invasion (FAO, 1961). Gibbon and Pain (1985) observed that the normal amount of seed needed per hectare was 30-60 kg, giving 150,000 plants per hectare. According to Mabhaudhi et al. (2013), it is traditionally cultivated in tropical environments by smallholder farmers with no access to both irrigation and fertilizers, who had little or no supervision on better production practices. The crop is also grown in small plots as monoculture (Ntundu, 1997; Manthe et al., 2002). The crop is further used in rotations, it may be cultivated as an opening crop possibly followed by cassava, or in the next year it may be intercropped with vegetables, groundnuts and/or other pulses or cereals. The crop grows well on deeply tilled land with a fine seedbed, ultimately permitting the plant to bury its developing fruits. Ridging is desirable if the soil is shallow or prone to water logging (Brink et al., 2006). Baudoin and Mergeai (2001) reported that appropriate loosening of the soil aids pod penetration and enhances the yield. Moreover, Tweneboah (2000) stated that a good seedbed is prerequisite to pod burying after fertilization. Earthing up of bambara groundnut is encouraged for better yields (Linnemann, 1987; Manthe et al., 2002; Fleissner, 2002).

Bambara groundnut yields are predominantly lower and unpredictable, due to the environmental and non-environmental traumas existing in their areas of cultivation. (Massawe et al., 2003; Muhammad and Massawe, 2015). Lack of improved varieties (70%) and drought (9.3%) were found to be the major and common bambara groundnut production constraints (Mohammed, 2014). However, even under optimum conditions yields are variable and unpredictable due to the variability among the landraces (Squire et al., 1996; Massawe et al., 2005). Absence of better varieties contributes to low yields; e.g. 400 kg ha^{-1} dry pods

relative to real harvests of about 3998 kg ha^{-1} dry pods (National Research Council, 1996). Variation in bambara groundnut yields have been observed: farm dry pods were in a range of 659 to 851 kg ha^{-1} (Linnemann and Azam-Ali, 1993), 457 to 3077 kg ha^{-1} (Vurayai et al., 2011b). Mabhaudhi and Modi (2013) found yield reduction due to insufficient water in three bambara groundnut landraces; Brown (2440 – 660 kg ha^{-1} (72%)), Red (3340 – 1520 kg ha^{-1} (54%)) and Light brown (3220 - 1430 kg ha^{-1} (56%)). Study by Chibarabada et al. (2015b) revealed reductions in seed mass per plant by 7%, 24%, 23% and 58% due to water scarcity in all four landraces; plain red, plain cream, brown speckled and black speckled respectively. Furthermore, it has been revealed that, dry pod yield can be as low as 300 kg ha^{-1} in poor environments and as high as 4200 kg ha^{-1} under good agronomic practices (Swanevelder, 1998; Collinson et al., 2000). The top five bambara groundnut producing countries in the world are: Burkina Faso, Cameroon, Mali, Niger and Democratic Republic of Congo. *Table 2.9.1* and *Table* 2.9.2 summarise the production trend of bambara groundnut from 2012 to 2017, with the total highest production of 184,010 tonnes obtained in 2016 (FAO, 2018c).

Table 2.9.1: Top five worldwide countries, bambara groundnut production (2012 -2014).

Country	Year									Total
	2012			2013			2014			
	Area (ha) x1000	Yield (tonnes) x1000	Average Yield t ha^{-1}	Area (ha) x1000	Yield (tonnes) x1000	Average Yield t ha^{-1}	Area (ha) x1000	Yield (tonnes) x1000	Average Yield t ha^{-1}	Yield tonnes x1000
Burkina Faso	57.45	65.12	1.13	48.83	56.56	1.16	44.61	51.09	1.15	172.77
Cameroon	42.96	34.78	0.81	43.39	36.64	0.84	43.82	38.20	0.87	109.61
Niger	51.54	22.47	0.44	70.40	32.68	0.46	70.51	32.38	0.46	87.53
Mali	35.24	23.48	0.67	37.06	20.94	0.56	37.70	22.93	0.61	67.35
Togo	18.60	6.03	0.32	21.61	6.33	0.29	20.60	18.57	0.90	30.93
DRC*	23.49	10.13	0.43	24.35	10.44	0.43	25.22	10.74	0.43	31.31
Total	229.27	162.01	0.71	245.65	163.58	0.67	242.47	173.91	0.72	499.50

*Source: FAO, (2018c), * Democratic Republic of Congo.*

Table 2.9.2: Top five worldwide countries, bambara groundnut production (2015 -2017)

Country	Year									Total
	2015			2016			2017			
	Area (ha) x1000	Yield (tonnes) x1000	Average Yield t ha^{-1}	Area (ha) x1000	Yield (tonnes) x1000	Average Yield t ha^{-1}	Area (ha) x1000	Yield (tonnes) x1000	Average Yield t ha^{-1}	Yield tonnes x1000
Burkina Faso	42.03	46.88	1.12	46.71	51.84	1.11	48.15	52.79	1.10	151.50
Cameroon	47.69	40.16	0.84	52.03	42.01	0.81	55.18	44.15	0.80	126.31
Niger	65.80	37.33	0.57	65.78	32.63	0.50	56.77	25.64	0.45	95.60
Mali	41.22	27.69	0.67	38.05	25.96	0.68	37.86	25.72	0.68	79.38
Togo	21.56	18.57	0.86	27.65	20.73	0.75	26.70	20.22	0.76	59.52
DRC*	25.44	10.76	0.42	25.81	10.85	0.42	26.34	10.99	0.42	32.60
Total	243.74	181.39	0.74	256.02	184.01	0.72	250.99	179.51	0.72	544.91

*Source: FAO, (2018c), * Democratic Republic of Congo.*

2.9.3 Importance of bambara groundnut

Bambara groundnut is the third in importance among cultivated legumes next to groundnut (*Arachis hypogaea* L.) and cowpea (*Vigna unguiculata*) (Azam-Ali et al., 2001; Mkandawire, 2007; Omoikhoje, 2008). Bambara groundnut seeds have a status of a whole meal, because of its substantial amounts of different nutritional contents; proteins (25%), carbohydrates (60%), essential amino acids (32.7% out of total amino acids) (Amarteifio et al., 2006). Report by CSIR, (2008) shows that, bambara groundnut has carbohydrate content as high as 43 - 69%. It can be used in various food products, such as vegetable milk. The crop also contributes to different medicinal purposes (Jideani and Diedericks, 2014; Yao et al., 2015). Bambara groundnut is important because of its ability to fix atmospheric nitrogen coupled with increased soil fertility for itself and other crops grown together or in cycles (Karikari et al., 1999). Availability of many and diverse bambara groundnut germplasms increases opportunities for better breeding programmes (Bioversity International, 2011; Hillocks et al., 2012). The ability of bambara groundnut landraces to produce yields in poor soils and in drought prone environments (Linnemann and Azam-Ali, 1993) points to the potential usability of this species.

Even though bambara groundnut has added benefits relative to other crops, it has not been given a priority by the research community; thus remains neglected as well as underexploited in their area of cultivation (National Research Council, 1996). It is considered as a neglected and underutilised plant species as it has been inadequately characterized and until recently, ignored by the research community (Oyeyinka et al., 2015). Many underutilised crops have been identified to have the potential to contribute towards improving food security (Massawe et al., 2016), improvement of economy of low-income families (Kahane et al., 2013). The status of neglected and underutilised crops resulted to dominance of unimproved cultivars. Although bambara groundnut is known for its varied genomic diversity, no deliberate efforts have been put forward to explore and use its potential with regard to cultivar/landrace evaluation and improvement (Massawe et al., 2005).

2.9.4 Drought resistance in bambara groundnut

Bambara groundnut is considered drought resistant (Tweneboah, 2000; Chibarabada et al., 2017). It is perhaps the most drought–resistant of the minor legumes (Collinson et al., 1997; Tweneboah, 2000; Chibarabada et al., 2017; Mabhaudhi et al., 2018; Fieldman et al., 2019). There is enough evidence that it is more drought resistant than its counterparts (Collinson et al., 1996; Vurayai et al., 2011a; Berchie et al., 2012). Furthermore, bambara groundnut has surpassed groundnut, a morphologically comparable species (Collinson et al., 1996). Still, no sufficient facts explaining how drought affects bambara groundnut (Mwale et al., 2007a; Jorgensen et al., 2011). The explanations regarding superiority of the crop to survive better under water deficit relative to other legumes are unclear (Collinson et al., 1993). Some reports recommends that, early maturing and deeper roots contribute to its ability to survive under dry conditions (Begemann, 1988). Moreover, drought resistance of bambara groundnut is

thought to be a consequence of osmotic modification and low transpiration (Collinson et al., 1997). Farmers claim that in years when groundnut performs worse because of lack of enough rainfall, bambara groundnut gives relatively better yields (Linnemann, 1990). Bambara groundnut landrace variation in reaction to drought have been informed (Collinson et al., 1996; Jorgensen et al., 2011; Chibarabada et al., 2015a, b; Nautiyal et al., 2017). Although bambara groundnut is known for its drought resistance, it is still negatively affected by drought. Regardless of the decrease in many yield related parameters of the crop, still bambara groundnut gave some yields under water stress conditions. Research relating to drought in bambara groundnut has been conducted, however, detailed information on drought resistance mechanisms are missing (Jorgensenet al., 2011; Sinefu, 2011; Vurayai et al., 2011a, b; Baroowa and Goigoi, 2012; Mabhaudhi, 2012; Berchie et al., 2012; Mabhaudhi and Modi, 2013; Mabhaudhi et al., 2013; Al Shareef et al., 2014; Ibraheem et al., 2014; Araus and Cairns, 2014; Araújo et al., 2014; Chibarabada et al., 2015a, b; Muhammad and Massawe, 2015; Muhammad et al., 2015; Chai et al., 2016; Nautiyal et al., 2017; Inuwa and Muhammad, 2017; Abejide et al., 2018). More studies on bambara groundnut therefore are needed for the purpose of resolving doubts on the following: i). Mechanism(s) used by bambara groundnut to yield where other crops fail completely ii). The main crop part(s) responsible for drought resistance.

2.10 Groundnut

2.10.1 Origin and history

Groundnut (*Arachis hypogaea* L.), likewise named earthnut, or goober, is a legume of the pea family (Fabaceae), cultivated for its eatable seeds. It originated from South America, grown between 40°N and 40°S (Janila et al., 2013). More than 50% of worldwide groundnut

cultivation take place in dry areas with unpredictable rainfall and without access to irrigation (Reddy et al., 2003). Groundnut is a key legume and oilseed cash crop mostly grown as a rain fed (Vaidya et al., 2015). Groundnut is a vital oleaginous foodstuff, broadly grown in tropical and semi-arid areas (de Lima Pereira et al., 2016). Together with the United States and China, Argentina is one of the main exporters of groundnut for human uses (USDA, 2011). Nevertheless, the crop production areas suffer intermittently periods of insufficient water supply almost each year (Collino et al., 2001).

2.10.2 Botany, ecology and production

Groundnut *(Arachis hypogaea* L.) is classified to the family Leguminosae and sub-family Papilionoideae (Waele and Swanevelder, 2001). *Arachis hypogaea* is from Greek words arachos and hypogaea, meaning weed and underground chamber, respectively (Adinya et al., 2010). Groundnut is a self-pollinated, annual (Tweneboah, 2000), allotetraploid (AABB genome, 2n = 4x = 40) (Krapovickas and Gregory, 2007). It is a geopcarpic crop, which produces pods underground (*Figure 2.10.1*). The pods are located to the depth of 7 to 10 cm (Ademiluyi et al., 2011). Groundnut emergence has two patterns. Epigeal emergence, whereby, hypocotyl elongates and cotyledons emerge above ground (as in soybean) and hypogeal emergence, whereby, cotyledons remain below ground (as in the case of field pea). Morphologically it is either erect or shrubby, with short branches or spreading form with elongated branches close to the ground.

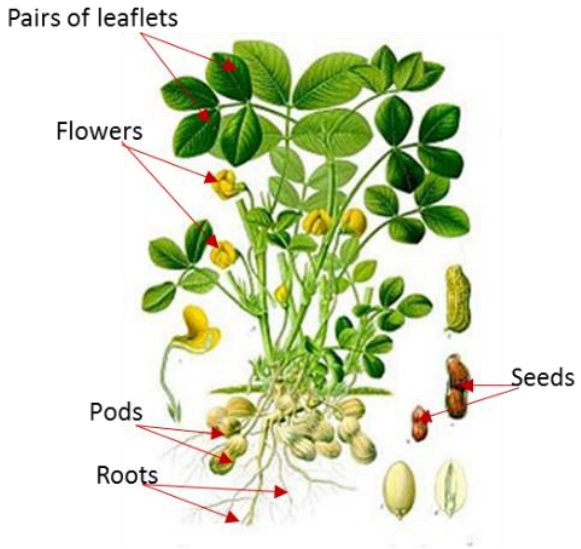


Figure 2.10.1: Morphological features of groundnut (*Arachis hypogaea* L.).

The stems of groundnut are tough, bear hairs and compound leaves with two pairs of leaflets. The flowers are found in the axils of the leaves and feature golden-yellow petals (*Figure 2.10.1* and *Figure 2.10.2*). The oblong pods have rounded ends and contains two or three seeds with constrictions between and a netted spongy shell. Depending on variety/landrace, the groundnut crop matures after 12 to 21 weeks. Harvesting of the crop is done when most of the leaves turned yellow and pods become hard (Arakama, 2013). Usually the crop takes 80 – 150 days from emergence to harvesting, depending on the variety (Oyelade et al., 2011). However, early maturing varieties have been found ready for harvesting even before 90 days after planting. As an essential tropical plant, groundnut needs extended and warm growing period (Weiss et al., 2000). The optimum day and night temperature for vegetative and reproductive growth and development in groundnut ranges from 25/25 to 30/26 ^{o}C and from 25/25 to 26/22 ^{o}C, respectively (Kakani et al., 2002). Groundnut productivity is low in the semi-arid tropics mainly due to drought caused by low and erratic rainfall (Nigam et al., 2001).


Figure 2.10.2: Groundnut plant showing: leaves and leaflets (left), flowers (middle) and pods (right).

2.10.3 Importance of groundnut

Groundnut is the thirteenth most vital food crop and the third major oilseed worldwide next to soybean and cotton, respectively (Taru et al., 2010; Nautiyal et al., 2011). Nutritionally the crop is a source of oil (44-50%), protein (20-35%), carbohydrates (10-20%), important vitamins and micronutrients (Varshney et al., 2009). The crop is not only used as a major edible oil but also utilised in the manufacturing of soap, cosmetics, shaving cream, and lubricants. Its kernels are used as processed foods like sweets, peanut butter and paste (Revoredo and Fletcher, 2002). Groundnut haulms, oil cake and leaves are used as animal feed and/or organic fertilizer (Kamara et al., 2011). The bi product obtained from shelling of groundnut is utilised as firewood and packing material for various organic and biological goods like charcoal, cork replacements and hard boards. The groundnut crop also is an important source of income to smaller holder famers (FAO, 2013b; Mangasini et al., 2013). As other legumes, it fixes atmospheric nitrogen and hence improvement of soil fertility.

2.10.4 Drought resistance in groundnut

Lack of enough water is the main abiotic stress that affects groundnut production and quality (Hamidou et al., 2012). More than 85% of global groundnut cultivation is in tropical and dry areas with limited soil moisture (Reddy et al., 2003; Hamidou et al., 2013). Hamidou et al. (2013) reported that crop losses due to water deficit stress are high and are associated with

increased temperatures. The crop generally encounters water deficit stress during growth and development, mostly flowering stage (Ming et al., 2017; Patel et al., 2017). In areas where water is a limiting factor, upright groundnut cultivars represent a significant alternative to farmers because of their short growing time and reduced water demand (Vorasoot et al., 2003; Painawadee et al., 2009). The drought resistance in groundnut depends on the growth habit. Groundnut has evolved morphological, anatomical, physiological, biochemical and molecular strategies to survive under water scarce conditions (Chaves et al., 2003). Groundnut is a relatively drought resistant crop through water-use efficiency mechanisms, which enables it to withstand water deficit stress periods of time (Nautiyal et al., 2002). Erect and early maturing groundnut genotype was suggested to be grown in semi-arid environments because of its high drought tolerance (de Lima Pereira et al., 2016). Valencia types (upright) possess roots that can penetrate into the deeper horizons and hence able to extract soil moisture under water limited conditions (Vorasoot et al., 2003). Shortening time to flowering is another tactic to survive under water scarcity and is an accepted criterion in evaluation of drought resistance in groundnut (Santos et al., 2013). Groundnuts have the ability to expand their roots to deep depths during drought. This contributes to ability of groundnut to survive under water limited conditions (Sanders et al., 1993). Groundnut roots also have the ability to go as deep as 180 cm (Allen et al., 1976) and as wide as 50 cm (Ketring and Reid, 1993). Apart from potential roots found in groundnut, proline also contributes to its drought resistance. Proline content is used as a measure of plant's ability against drought as proline accumulation aids osmotic balance under water deficit conditions (Vaidya et al., 2015). During water stress periods, groundnut accumulates very high amounts of proline in the leaves (Jharna et al., 2001; Ramanjulu and Bartels, 2002) which makes it resistant to drought.

2.11 Response of bambara groundnut and groundnut under unfavourable conditions

Bambara groundnut is undoubtedly the most drought–resilient of the legume crops (Tweneboah, 2000; Mazahib et al., 2013) with great potential as an alternative legume to groundnut and soybean (*Glycine max* L.), which cannot withstand harsh conditions (Mazahib et al., 2013). Different days to maturity have been observed in both species. For instance, different ranges of days from sowing to maturity have been reported in bambara groundnut; 150-180 days (Hillocks et al., 2012), 119-128 days (Mabhaudhi et al., 2013), 129-141 days (Atoyebi et al., 2017), 147 days (Mwale et al., 2007a). Similarly, different days to maturity have been reported in groundnut; 102 -141 days (Rowland et al., 2006), 90- 165 days (Madhan and Nigam, 2013), 92-122 days (Dapaah et al., 2014). However, groundnut showed less days to maturity compared to bambara groundnut. This indicates that, on average groundnut matures earlier than bambara groundnut and hence more favoured to escape drought.

Unfortunately, limited information is available to support bambara groundnut drought resistance superiority over its comparator. In a study conducted by Kumaga et al. (2003), groundnut performed better than bambara groundnut, which contradicts other studies for instance Mazahib et al. (2013). In the same experiment by Kumaga et al. (2003) insufficient soil water supply significantly decreased growth of both bambara groundnut and cowpea but not groundnut.

According to Linnemann and Azam-Ali (1993); Thottappilly and Rossel (1997) bambara groundnut is considered superior under harsh conditions over groundnut. On the other hand, findings by Wassermann et al. (1984) did not support the general belief held by Hepper (1970) and Doku and Karikari (1971) that bambara groundnut is more resistant on nutrient poor soils as compared to groundnut. In fact, the findings showed the opposite. In the field trial, the

groundnut revealed nearly no response to lime on an acid soil very low in calcium, whereas bambara groundnut showed high response. The experiment conducted by Wassermann et al. (1984), revealed that bambara groundnut is not as acid resistant as the groundnut and that soil calcium level is of great importance for pod development in bambara groundnut as compared to groundnut. Other studies by Munns and Fox (1977) reported that, common groundnut is known for its good adaptation to acid soils. These contradictory findings call for more comparative experiments between the two legumes.

2.12 Physiological responses of plants to drought

2.12.1 Gaseous exchange

Stomata are the small apertures on plant leaves and stalks which are surrounded by two guard cells. They are responsible for gaseous exchange between plant's shoot and the atmosphere (Zhao et al., 2015). Stomatal conductance measures the rate of carbon dioxide absorption (assimilation) and amount of water loss (transpiration). Rate of gaseous exchange is determined by the size (open and close) of stomatal aperture (Aminian et al., 2011; Busch, 2014). Hence, gas exchange, depends on number, magnitude as well as plasticity of the stomata aperture; the higher the stomata aperture the higher the stomatal conductance, and consequently increased transpiration and photosynthesis. The hand instrument for measuring stomatal conductance (Decagon SC-1 Leaf Porometer, Decagon Devices Incorporation, USA) gives quick measurements of gaseous exchange on plant leaves under well water supply, whereas the readings under water deficit plants (leaves) take some time (Pietragalla and Pask, 2012). Stomata are organized cells which respond to environmental and internal-plant changes and modify shape to permit gas exchange. Stomata control carbon dioxide absorption and transpiration and as such they are very important in photosynthesis, leaf

cooling and nutrient absorption from the soil solution (Farooq et al., 2009). In order to balance soil moisture absorption and leaf-water loss, regulations in stomata is a key mechanism for plants survival. Stomata closure causes reduced transpiration, means low cooling of the plant leaves, reduced soil water and nutrient.

Closing of stomata is a result of reduced turgor pressure in the guard cells (Outlaw, 2003). Collinson et al. (1997) suggested that drought resistance of bambara groundnut is caused by osmotic regulation and/or reduced water loss due to closing of stomata. Reduced CO_2 diffusion and fixation, and subsequently reduced photosynthesis, are all consequences of stomatal closure. Numerous mechanisms and signalling pathways have been associated with stomatal closure during adverse conditions (Arve et al., 2011). Abscisic acid (ABA) is the major and best-known signal that encourages stomatal closure (Nemhauser et al., 2006; Huang et al., 2008). Closing of stomatal by hydro passive pathway occurs when the evaporation of water from the guard cells is too low to be balanced by movement of water into guard cells (Arve et al., 2011). The amount of water in the cells surrounding the stomata quickly decreased to the threshold level and the cells contract (Luan, 2002). Another signalling pathway leading to closing of stomata is active stomatal closure; in this ABA together with elevated levels of CO_2 triggers indicating ways causing closing of stomata (Kim et al., 2010). The active stomatal closure is achieved by the extrusion of anions from guard cells (Arve et al., 2011; Brodribb and McAdam, 2011). During the process of stomatal closure, various secondary messengers are involved; like Ca^{2+}, H_2O_2 and NO (Garcia-Mata and Lamattina, 2009). Closing of stomatal has undesirable effects on CO_2 assimilation, photosynthesis rate, transpirational cooling, soil moisture as well as soil minerals absorption. Therefore, prior opting for mechanisms that will lead to stomatal closure, it must be clear that, the advantages

gained from reserved water offsets its adverse impacts (Arve et al., 2011). Mwale (2005) reported a reduction in stomatal conductance due to water deficit. Collinson et al. (1997) testified changes of stomatal conductance (gs) from 0.46 - 0.79 cm s^{-1} in well-watered bambara groundnut plants to 0.13 - 0.48 cm s^{-1} in the water deficit stressed plants. A study on bambara groundnut landraces by Muhammad et al. (2015) showed that, there was a continuous reduction in stomatal conductance after periods of water deficit.

Photosynthetic rate is extremely affected by insufficient water supply because of decrease in leaf development, reduced photosynthesis process, early drying of leaves and reduced biomass production. Anjum et al. (2011) detected a substantial decreased photosynthetic rate (33%), transpiration (38%), CO_2 and water vapour movement (25%), ability to utilise available water (51%) as well as internal CO_2 (6%) under water limited maize plants relative to well-watered plants. A combination of stomatal and non-stomatal restrictions was revealed to reduce photosynthetic activity in water scarce conditions (Del Blanco et al., 2000; Samarah et al., 2009). Farooq et al. (2008), on the other hand, informed slight restrictions to photosynthesis caused by stomatal mechanisms relative to non-stomatal mechanisms. Stomata closure under insufficient water supply, is one of the first reactions of plants exposed to insufficient water supply conditions. On the other hand, non-stomatal limitations involve fluctuations in chlorophyll production, chloroplast metabolism, and disturbance in build-up, transportation, as well as dissemination of plant assimilates (Farooq et al., 2008).

Insufficient water supply affects vital ingredients (such as chlorophyll, carotenoids) of photosynthesis (Anjum et al., 2003). According to Fu and Huangi, (2001), insufficient water supply caused injuries to photosynthesis machinery, reduced Calvin cycle enzymatic performance, as well as decreased final harvests (Monakhova and Chernyadev, 2002).

Furthermore, limited water supply varied the normal fractions of the photosynthetic pigments (Anjum et al., 2003; Farooq et al., 2009). Sunflower plants revealed a significant decrease in chlorophyll under severe water deficit conditions (Kiani et al., 2008). Manivannan et al. (2007) reported similar results in the same crop (sunflower). Decline in chlorophyll content in high water scarcity conditions is the main causative of photosynthesis inactivation (Anjum et al. (2011). Imbalance among the manufacture of reactive oxygen species (ROS) and antioxidant (like proline) protection is known to affect photosynthesis (Reddy et al., 2004). This imbalance favours ROS while denaturing proteins, lipids and important components at cellular level.

2.12.2 Compatible Osmolytes

Compatible osmolytes are strong osmoprotectants that counteract the effects of osmotic stress. Plants are exposed to various forms of environmental stress. Among these stresses, osmotic stress, caused by water deficit and salinity is of greatest importance. It retards plant growth and reduces crop production (Boyer, 1982). Most of plants gather compatible osmolytes, for instance proline, sugar alcohols and glycine betaine when under water deficit or salinity (Chen and Jiang, 2010; Liang et al., 2013). It has been reported that compatible osmolytes do not obstruct normal biochemical activities and act as osmoprotectants during osmotic stress. Most known compatible solutes are amino acids (notably proline) and quaternary ammonium compounds. Nevertheless, proline is possibly the abundantly available osmolyte.

Proline and other compatible osmolytes, share the characteristic of being uncharged at neutral pH, and solubilizes easily in water (Ballantyne and Chamberlin, 1994). Furthermore, at high concentrations they have little or no adverse effect on macromolecule-solvent associations (Yancey, 1994). Proline plays a significant function of regulating plants'

cytoplasmic osmotic in reaction to osmotic stresses (Wyn Jones et al., 1977). Proline is collected by leaves of various halophytic higher plant species planted in saline soils. Proline defends membranes and proteins against increased accumulation of harmful compounds as well as high temperatures (Santoro et al., 1992). Proline is also responsible for scavenging destructive groups of ions (e. g. hydroxyl groups) (Smirnoff and Cumbes, 1989). However, there is still lack of clarity on whether proline accumulation is a sign of adaptation against stress or symptom of stress. What is clear is the fact that proline build-up is known to occur under insufficient water supply conditions (Hare et al., 1998). Vurayai et al. (2011a) showed that water stress increased proline concentration in bambara groundnut plants, compared with non-stressed plants. Studies on bambara groundnut by Muhammad et al. (2015) revealed that, concentrations of proline increased to some extent following three weeks of insufficient water supply. Increases in the proline concentrations were experienced under water deficit and osmotic stress conditions (Gomes et al., 2010; DaCosta et al., 2011). Proline production and accumulation is associated with resistance to various stresses; it has been suggested to be an important trait in screening plants against wilting and salinity (Gibon et al., 2000).

2.12.3 Leaf Relative water content

The relative water content (RWC) of a leaf is the measure of real water present in a leaf in relation to its maximum water holding ability. It is a main indicator of hydration status in plants; it reveals the gap or imbalance between water in the leaf tissue and water transpired (Lugojan and Ciulca, 2011). RWC measures the shortage of water in plant leaf and also indicates the level of stress following insufficient water supply or increased temperature. Relative water content incorporates plant leaf water energy (ψ), with the effect of osmotic

adjustment. Similar to ψ, leaf RWC indicates plant's reaction to various environmental conditions. However, RWC is more stable compared to ψ (Sade et al., 2009; Sade et al., 2012). Variety which is able to preserve water in leaves under limited water supply will always be physiologically favoured (Sade et al., 2012).

In an experiment in bambara groundnut, it was revealed that, RWC ranged between 92-96% under well-watered treatments whereas under water deficit treatments it dropped up to 83% (Collinson et al., 1997). Mwale (2005) reported no effect of water deficit stress on RWC; neither RWC values for well irrigated plants nor droughted plants found to have values below 90%. In another experiment involving groundnut and bambara groundnut by Nuer (1989), results showed that, RWC in groundnut was 79% under well irrigated plants and 50% under water deficit plants. On the other hand, RWC in bambara groundnut was 83% and 70% for control and droughted treatments respectively. Prolonged high temperatures increased rate of water loss through leaves leading to reduced relative water content (Farkhutdinov et al., 2003). Hayatu et al. (2014) reported decreased leaf area, RWC and yield of cowpea due to water deficit stress. It was revealed that, RWC continue to decline as a result of imposition of drought to bambara groundnut plants (Muhammad et al., 2015).

2.12.4 Leaf chlorophyll content

Chlorophyll is a photosynthetic pigment to the plant (Taiz and Zeiger, 2006). Its functions and characteristics include; it offers the green colour to plants, it captures (absorbs) sunlight energy and largely determines ability of plants to photosynthesise (Kamble et al., 2015). Leaf chlorophyll concentration is often measured as an indicator of amount of chloroplast, of photosynthesis activity and of plant metabolism (Kamble et al., 2015). Chlorophyll is kept in the chloroplast of green leaf plants and mostly it is found in the green areas of shoots and

roots (Srichaikul et al., 2011; Mirza et al., 2013). Nonetheless, chlorophyll synthesis is largely dependent on sun light and it is the key harvesting molecule of energy for plants (Srichaikul et al., 2011). Photosynthetic pigments enable plants to absorb energy from light, so leaf chlorophyll content is an important factor influencing the capability of plant photosynthesis (Taiz and Zeiger, 2006). Numerous reports have clarified that limited water supply substantially reduces chlorophyll content of various crop species (Mafakheri et al., 2010; Gholamin and Khatnezhad, 2011). The amount of chlorophyll in leaf tissue is influenced by nutrient availability and environment stresses like drought, cold, heat and salinity (Jiwan, 2009). Though, the existence of low levels of chlorophyll in leaves (chlorosis) is a common indication of stress and might be poorly associated to water status in the field when there is interaction of other environmental complications.

Chlorophyll absorbs red and blue wavelengths while reflecting green wavelengths and hence the unique green colour to plant leaves. Chlorophyll is also known as 'photoreceptor' because it absorbs sun light. The concentration of chlorophyll can directly affect photosynthetic potential as the quantity of solar energy absorbed by a leaf is essentially a function of the concentration of photosynthetic pigments (Filella et al., 1995). The concentration of chlorophyll generally decreases and that of carotenoids increase under stress and during senescence (Peñuelas and Filella, 1998); therefore amount/concentration of chlorophyll can directly be associated with plant leaves water status.

Leaf chlorophyll concentration can be rapidly and non-destructively measured by SPAD chlorophyll meter (Richardson et al, 2002; Akkasaeng et al., 2003). There is a positive association with regard to SPAD readings versus chlorophyll content obtained from laboratory extraction method (Murillo-Amador et al., 2004; Cornelissen, 2005). Insufficient water to

plants has been reported to reduce concentration of chlorophyll in various crop species involving, wheat (Talebi, 2011), and maize (Gholamin and Khayatnezhad, 2011; Khayatnezhad et al., 2011). Nevertheless, there is limited literature describing the relationship between leaf chlorophyll content and drought resistance in bambara groundnut. A study by Vurayai et al. (2011a) revealed that water deficit stress did not significantly reduce leaf chlorophyll content in bambara groundnut plants. However, in the same experiment by Vurayai et al. (2011a), chlorophyll content was found to decline after imposition of water deficit stress during flowering. Mabhaudhi et al. (2013) reported no significant differences due to water deficient in bambara groundnut landraces. Muhammad and Massawe (2015) revealed that, there was significant decrease in chlorophyll content when bambara groundnut was subjected to limited water supply.

Various experiments on chlorophyll have revealed existence of positive relationship between water deficit stress and chlorophyll content in groundnut crop. For instance genotypes exposed to severe water deficit stress had darker leaf colour and higher SPAD chlorophyll (due to reduced leaf surface area) relative to well-irrigated plants (Songsri et al., 2009). Chlorophyll stability has been proposed as a measure of insufficient water resistance in peanut (Arunyanark et al., 2008). Furthermore, a positive relationship was reported between transpiration efficiency (which is an important determinant for yield) and SPAD leaf chlorophyll concentration in peanut (Sheshshayee et al., 2006).

2.12.5 Roots under drought stress

Massive and long root systems are beneficial during initial stages of growth and also in absorption of soil moisture in deeper layers under limited water supply to cover the leaf water loss (Shakeel et al., 2011). The responses of roots to water deficit stress are unclear. An

increased root growth as a result of water deficit stress was observed in *Catharanthus roseus* (Jaleel et al., 2008). However, root development was not significantly restricted in water limited maize plants (Sacks et al., 1997). Limited water supply has been reported to favour root growth rather than shoot growth due to the fact that, roots are not as sensitive as plant shoots (Wu and Cosgrove, 2000). Under insufficient water supply plant roots alert shoots through xylem triggering variations in plants physiology followed by mitigation mechanisms against the prevailing adverse condition. Abscisic acid (ABA), cytokinins, ethylene, malate and other unnamed factors are responsible for root–shoot signalling (see for example; Guerrero and Mullet, 1986; Schachtman and Goodger, 2008; Tombesi et al., 2015; Sah et al., 2016). The initial response to this alert/signalling is stomatal closure. Abscisic acid promotes movement of potassium ions from the guard cells followed by loss of turgor pressure and ultimately closing of stomata. Desiccation of plant leaves has been reported to increase Abscisic acid levels (50 fold) due to severe decrease in turgor pressure (Guerrero and Mullet, 1986). Furthermore, ABA's main function (root to shoot messenger) received a challenge from experiments. In water stressed plants the concentrations of ABA in the xylem liquid were significantly lesser relative to the applied (exogenous) ABA concentrations needed for stomatal closure in detached plant leaves (Munns and King, 1988). Although there is other factors associated with monitoring plant growth and development, Abscisic acid is the main signal. Next to ABA, Cytokinin in the roots also moves to the shoot parts under water deficit stress conditions. Cytokinins produced by roots are involved in plants' nutrient withdrawal (Schachtman and Shin, 2007). Sakakibara (2006) suggested cytokinins to be important in drought responses since they are produced mostly in roots.

Among other root traits, rooting depth is one of the most often assessed traits. This is due to the fact that, crops with deeper roots have ability to access water and nutrients in the deeper soil layers (Wasson et al., 2012). Other root traits include; total length, surface area, average volume plus diameter (Chen et al., 2016; Zenis et al., 2016). The main focus of plant breeding programmes worldwide is to develop plants with ability to grow and continue productive in poor soils. Identification of root traits and phenes that assist the investigation and effective use of water and nutrients can be used to attain current breeding objectives. However, the challenge of phenotyping belowground traits with higher throughput has hindered progress in the study of plant roots (Paez-Garcia et al., 2015).

Zenis et al. (2016) reported significant reduction in various soybean root traits (namely length, surface area, average diameter and average volume) due to insufficient water supply. Xiong et al. (2006) informed that growth of lateral roots in mouseear cress (*Arabidopsis thaliana* (L.)) was significantly decreased due to insufficient water supply. Study by Garay and Wilhelm (1982) revealed accumulation of roots in the top 15 cm of the soil profile due to early water deficit. Nevertheless, as the limited water supply continues over time, plant roots were found to accumulate more at 90 cm to 120 cm depths; which indicates that the roots grew deeper to absorb water and minerals. The structure and development of the root system mostly governs crop role under water deficit conditions. For instance, Pandley and Shukila (2015) reported that, under slight water deficit stress, the root growth is usually maintained while shoot growth is inhibited. The higher root biomass is a result of assimilate distribution. Decrease in photosynthesis, disruptions of production of carbohydrates as well as concentration of sugars in leaves are consequences of inadequate soil moisture (Farooq et al., 2009). Several factors including water deficits and carbon dioxide influence biomass allocation

(Wilson, 1988). Among carbohydrates, sucrose plays a key role in biomass partitioning between shoots and roots (Farrar, 1996; Lemoine et al., 2013). In leaves, hexoses are converted to sucrose by sucrosephosphate synthase and sucrose synthase (Huber and Huber 1996). Sucrose synthase is mostly present in roots and other sink tissues, where it is part of sucrose utilization pathways (Wind et al., 2010). Hence increased root growth compared to shoot (source), which even the reduced assimilates in the shoot has to be exported to sink tissues.

2.13 Phenotyping for drought resistance

Plant phenotyping targets at a quantification of quality, photosynthesis, development, architecture, biomass productivity of single plants or plant stands by means of broad variety analysis protocols (Walter et al., 2012). It represents an indispensable means to explore physiological principles responsible for important roles associated with plant parts and for selecting superior genotypes in plant improvement programmes (Walter et al., 2012). Over the previous years, different phenotyping tools (e. g. phenomic tools) have been used in both laboratory and field environments (Sinclair et al., 2014). Although substantial development on improvement of phenotyping tools (e.g. imaging tools) of above ground plant parts have been achieved, the related data processing and bioinformatic requirements still a problem (Furbank and Tester, 2011; Araus and Cairns, 2013). Furthermore, regardless of extensive struggles, phenotyping protocols or methods fully appropriate for real world (actual field) enviroments, are in stage of prototype (Furbank and Tester, 2011; Araus and Cairns, 2013). Therefore, typical guide methods for phenotyping of plants remains an important crop improvement tool (Beebe et al., 2013). Typical guide techniques/methods are important in developing countries of Africa where research infrastructure is limited. Shoot morphological

characteristics are usually used for plant phenotyping (Manavalan et al., 2009). Above ground plant traits are easy to investigate under field environments. Leaf movement (Pastenes et al., 2005), leaf flagging, shedding and leaf area reduction (Blum, 2005) are normally used in screening for drought resistance. Leaf orientation traits (leaf rolling/folding) are infrequently used in screening/selection for drought resistance, due to the fact that, they are not easy to quantify (Kanagaraj et al., 2010; Salunkhe et al., 2011). Generally, plant physiological evaluation and selection techniques are not commonly used because of their high cost, high time-demanding and also are complicated.

Roots are the earliest plant part to respond to insufficient water supply. However, phenotyping of roots is seldom done, mainly in real world environments (Amoroso et al., 2010). The distribution of roots in the deeper soil layers, is responsible for determination of plants' ability to capture water and plant nutrients (Zhao et al., 2004). Hence, architecture of roots, determines the general plant performance (emergence/establishment, development as well as final harvest). The response of root system architecture to insufficient water supply have been undertaken in various support media; e. g. hydroponics and agar plates (Manavalan et al., 2010; Trachsel et al., 2011; Prince et al., 2013). Nevertheless, few experiments have been conducted to study root parameters for selection of improved nutrient (e. g. nitrogen) use efficiency or improved water use efficiency. The application of current operational root phenotyping techniques (e. g. use of phenomic technologies) in marker-assisted selection are hindered by lack of ability to study roots in field environments. Common root phenotyping methods applied in the field (e. g. use of soil cores and application of typical soil excavation procedures (sholvemics)) remains the best methods for measuring various root traits (Nielsen, 1997; Trachsel et al., 2011). However, soil cores and sholvemics methods do to offer detailed

information of root architecture, anatomy (e.g. abundance of root hairs) or function (e.g. nutrient absorption). Furthermore, techniques like shovelmics are labourious and time consuming without preserving the spatial architecture of the roots (Reubens et al., 2007).

Thus, recognising crop species or genotypes having improved root traits still an important problem to plant biology, particularly under field conditions. Root orientation is significantly altered when subjected to insufficient water supply, favouring the production of massive roots for enhanced overall root surface area and hence amplified soil moisture and nutrients uptake (Osmont et al., 2007). Together with plans that reduce water loss through transpiration, (like closing of stomata, rolling and or shedding of leaves), an increase in root mass predominantly deeper in the lower soil layers increases plant water status. Superior root phenotypes are nowadays suggested to be main to improved drought resistance traits for improvement of overall crop performance, e. g. soybean (Agbicodo et al., 2009; Lopes et al., 2011). Soybean crop has shown genetic variability for root architecture and morphology, involving traits like root angle, root diameter, root length, root surface area and root depth (Zhao et al., 2004; Ao et al., 2010). Massive and deeper roots are known to promote soil moisture extraction particularly at deeper depths (Garay and Wilhelm, 1982; Zhao et al., 2004).

In the efforts to study roots, alternative approaches have been employed including the use the root-box pin board method, soil filled glass rhizotrons, the basket method, use of phenyl vinyl chloride (PVC) columns (Shashidhar et al., 2012). Although these methods do not represent real field conditions, they explore more root parameters that are related to drought resistance as compared with direct field conditions. These parameters reflect their performance in real field conditions. PVC columns have been used with varying soil depths

(Amoroso et al., 2010). PVC columns can be used in both field and controlled environments (Shashidhar et al., 2012). Soil moisture stress can be imposed in different ways, e. g with a rainout shelter covering the area under study, or conducted in nearby field using the similar treatments. PVC columns are considered as better equipment used in root studies. Any number of genotypes can be investigated using this method, depending on the space and tubes available. Thus, breeding for drought resistance varieties based on deep rooting pattern can be carried out. From PVC column experiments, both shoot and root traits can be determined. Specifically for root traits; maximum root length, root number, average root diameter, root surface area, root volume can be measured. Limited information is available for the reaction of groundnut genotypes to water deficit stress for root systems (Songsri et al., 2009) and for bambara groundnut (Karunaratne et al., 2009). However, root responses to drought can be an important mechanism to maintain high pod yield and can be used as a selection criteria for drought resistance in both legumes. A better understanding on how groundnut and bambara groundnut landraces respond to drought using root traits is important for drought resistance cultivars. Therefore, it is crucial to evaluate root characteristics related to drought in both bambara groundnut and groundnut. This information is helpful to determine future strategies for bambara groundnut and groundnut breeding in water scarcity areas.

2.14 Chapter summary

This chapter provides a detailed review of relevant literature on bambara groundnut and groundnut crops. Bambara groundnut is an underutilized crop with superior agronomic values, such as drought resistance and yield resilience under low input system, and it also emphasized the potential of bambara groundnut as a future crop. There exists a knowledge

gap in understanding the mechanisms and indices responsible for drought resistance in bambara groundnut and groundnut crops. These gaps were the focus of the next chapters.

CHAPTER THREE

Materials and Methods

3.1 Introduction

Field and rainout shelter experiments were conducted to study the effect of soil moisture deficit stress on bambara groundnut (*Vigna subterranea* L. Verdc) and groundnut (*Arachis hypogaea* L.). This chapter presents materials and methods common to chapters Four, Five and Six. Details of procedures, which are unique to specific experiments, are included in the respective materials and methods sections of the individual chapters where the experiments are presented.

3.2 Experimental sites

Three field experiments were conducted in Mtwara, Tanzania at two Naliendele Agricultural Research Institute (NARI) experimental sites (site 1 located at S10°35'27.2'', E040°16'86.5'', 103 meters above sea level and site 2 located at S10°35'52.2", E040°17'75.3", 84.0 meters above sea level). Site 1 (Mizambaraoni) was used for the experiments, one (2015/2016 dry season) and two (2016/2017 dry season) while site 2 (Mpakani) was used to conduct the third field experiment during 2016/2017 dry season. Both experimental sites were originally planted with cashew nut. The area has unimodal type of rainfall, which normally starts at the end of December and ends in May (Sumner, 1983; Kabanda, 2018; https://weather-and-climate.com). Bambara groundnut and groundnut are normally grown during the rainy season.The environmental data for all field experiments were recorded at Naliendele Agricultural Research Institute weather station, which is located about 1500 m and 3000 m from site 1 and site 2 respectively.

Two rainout shelter experiments were conducted in the rainout shelter, at the University of Nottingham Malaysia (UNM) (GPS: 02°94'65.98'', 101°87'37.75'' and 56 metres above sea level), in Semenyih, Malaysia. The first experiment was carried during the 2016/2017 cropping season while the other one was conducted during 2017/2018 cropping season. Environmental conditions in the rainout shelter, which included relative humidity, photosynthetically active radiation (PAR) and atmospheric temperature, were recorded throughout the experimental period using a mini weather station (Watchdog 2000 Series, Spectrum Technologies, Plainfield, IL, USA).

3.3 Treatments

3.3.1 Plant materials

Four landrace-derived genotypes of bambara groundnut and one groundnut variety were used in the different experiments carried out during the research work. For the sake of reporting, it has to be noted that, both "landrace-derived genotypes" and "variety" will be referred as "landraces" from here on. The landraces used in the present study are shown in *Table 3.3.1.* S19-3 was selected based on its known ability to withstand drought (Jorgensen et al., 2011) while selection of the other landraces was based on their yield performance.

Table 3.3.1: List of plant materials used for the studies, their source and drought tolerance status

Landrace-derived genotype/variety	Crop	Drought Status	Source/Origin
NALBAM 2	Bambara groundnut	Unknown*	Naliendele/Tanzania
NALBAM 4	Bambara groundnut	Unknown*	Naliendele/Tanzania
DodR	Bambara groundnut	Unknown	UNM/Dodoma, Tanzania
S19-3	Bambara groundnut	Drought resistant^{+}	UNM/Namibia
MNANJE	Groundnut	Unknown*	Naliendele/Tanzania

* NARI, (2013), $^{+}$Jorgensen et al. (2011).

The groundnut, MNANJE, is highly preferred by market because of its large seeds, high oil content and tolerance to rosette disease (NARI, 2013). NALBAM 4 and NALBAM 2 are relatively high yielders, both have semi bunch growth type (IPGRI, 2000) and relatively late maturing (NARI, 2013). DodR has a spreading type of growth (IPGRI, 2000). The drought resistance status of NALBAM 4, NALBAM 2 and DodR is not known. S19-3 has bunch type of growth (IPGRI, 2000) and is known to be drought resistant and early maturing (Jorgensen et al., 2011).

Figure 3.3.1: Bambara groundnut and groundnut seeds used during the course of the experiments

3.3.2 Water regimes

In both field and rainout experiments, the same watering method and regimes were applied. Treatment 1 was 'well irrigated' throughout the growing period, maintained at 100% field capacity; in treatment 2 water deficit stress was imposed at the start of flowering to the end of first flush flowering. In treatment 3 water was withheld during the pod development stage (first pod appearance until the full seed (R6=reproductive stage six)).

3.4 Experimental design and layout

In all experiments, (field and rainout shelter), the experimental design used was a split plot in a randomized complete block design (RCBD) replicated thrice. Treatments involved three watering regimes and four landraces. It is worthy to note that, the first field experiment (2016 dry season) used two bambara groundnut landraces (NALBAM 2 and NALBAM 4) and one groundnut landrace (MNANJE); NALBAM 2 was only used in the first field experiment. In the successive experiments, two in the field and two in the rainout shelter, all experiments used the same three bambara groundnut (DodR, NALBAM 4 and S19-3) landraces and one groundnut (MNANJE) landrace. Watering regimes were assigned to the main plots whereas landraces were assigned in sub plots.

3.5 Common measurements for both field and rain out shelter experiments

Field and rainout shelter measurements involved both destructive and non-destructive data collection as described in the following sub sections. As plants progressed, the seedlings were observed physically for any disorders, evidence of wilting and any other possible changes throughout the respective experimental periods. Physiological measurements were taken before the imposition of water deficit stress, during the water deficit stress, at the end of water deficit stress and for some parameters after water deficit stress.

3.5.1 Growth data

With exception of days to maturity, other stages were monitored according to description by the IPGRI (2000) manual. *Days to emergence* was observed by monitoring the number of days elapsed from sowing to the emergence of seedlings. *Days to flowering* was taken as the number of days elapsed since seed emergence to first appearance of a flower in a given sub plot. *Days to 50% flowering* was determined by recording the number of days following

emergence until half of plants in a plot had at least one open flower. *Days to podding*, was calculated as the time taken from emergence to first appearance of a pod in a given sub plot. *Days to maturity*, was calculated as the time taken from seed emergence to physiological maturity (https://www.maximumyield.com). Plant height was measured from ground level to the tip of the highest point, including the terminal leaflet. Plant canopy spread was taken as the widest length between two opposite sides.

3.5.2 Relative water content (RWC)

RWC measurements were carried out before drought, at mid-treatment of drought, at the end of drought and after recovery. Youngest full-expanded middle leaflets were used for samples. Two leaflets were collected randomly from each plant and punched with a steel borer. This was carried out as described by Vurayai et al. (2011a). Leaflets for RWC measurement were sampled around midday. Fresh weight of the leaflet disc was obtained by weighing the leaf discs immediately after punching from the plant leaves. To obtain turgid weight, leaflet discs were incubated in distilled water at low light intensities (Schonfeld et al., 1988) for 24 h. Dry weights of leaflet discs were obtained by oven drying at 75 ^{o}C for 48 h. The leaf relative water content was then calculated from the relation below; as described by Barrs and Weatherly (1962); Schonfeld et al. (1988).

$$\mathrm{RW}(\%) = \left(\frac{\mathrm{FW}-\mathrm{DW}}{\mathrm{TW}-\mathrm{DW}}\right) * 100 \qquad \text{.....} \textit{Equation 1}$$

Where: FW = fresh weight of leaf samples; TW = turgid weight of leaf samples; DW = dry weight of leaf samples.

3.5.3 Leaf chlorophyll content index

Leaf chlorophyll content index was measured non-destructively using a SPAD-502 plus chlorophyll meter (Spectrum Technologies, Illinois, and USA) (Richardson et al., 2002). Measurements were made on three youngest fully expanded leaves on each plant and then averaged to represent the chlorophyll reading for that plant. Soil plant analysis development (SPAD) measurements were always done in the morning, beginning from around 8.00 am. The chlorophyll content was expressed as Chlorophyll content index (CCI).

3.6 Field experiments

3.6.1 Experiments layout

In all three-field experiments conducted, there were three replications each containing three main plots. The sub plot size was 4 m long by 4 m wide with 8 rows. Main plots were spaced at 2 m apart, while plant spacing of 0.5 m between rows and 0.3 m within the rows was used.

Figure 3.6.1: Field layout of experiment 1 (27 days after sowing) at Naliendele agricultural Research Institute during 2016 cropping season.

3.6.2 Cultural practices

Characterization of soil nutrients status in the experimental field was done prior to any other activity. The textural class was loamy sand. According to UNESCO/FAO Classification, the soil in the area is classified as *Ferralic* Cambisols (Mowo et al., 1993). The land was ploughed, harrowed and levelled prior to planting using a tractor, followed by plot demarcation. One day before sowing, all plots were normally saturated with water in order to attain equal soil moisture content across the plots. Soil moisture content at field capacity (FC) was obtained by calculating amount of moisture in the soil one day after the soil was saturated with water. This was done by using gravimetric soil moisture determination method (see equation 5, in Chapter 4). Two seeds per hole were planted at a depth of 3-5 cm using the dibbling method. Seedlings were thinned to one 10 days after emergence. Weeds were controlled manually using hand hoe as need arose. Plants were irrigated using a watering can. Control plants and other plants which were not under water deficit stress, at a given time period, were normally irrigated when the soil moisture dropped below field capacity. Changes in moisture content were determined by measuring the soil moisture content gravimetrically for field experiment 1 and PR2/6 (Delta T Devices, UK, 1971) soil moisture probe for field experiments 2 and 3. Watering was done once daily during evening. Watering of plants depended on both environmental conditions and available soil moisture content. Normally, each row was supplied with 10 l (1000 ml per plant) of water per watering round. Weeding was done twice by using hand and hand hoe. Fertilizer and herbicide application are described under specific experiments.

3.6.3 Data collection

3.6.3.1 Stomatal Conductance

Stomatal conductance was measured with a Decagon Device Leaf Porometer SC-1 (Decagon Devices Incorporation, USA). Measurements were taken around 12 noon to 2 pm, on three fully expanded leaves of three plants per treatment per replication.

3.6.3.2 Root architecture

Root excavation technique was adopted from Trachsel et al. (2011). Two representative plants for each sub plot were selected for excavation, measurements and visual scoring. Only fully bordered plants were selected. Roots of the plants were bulked for visual scoring and only a single rating was recorded. This technique required taking the whole root with the whole plant. This was achieved by excavating the soil alongside the plant (*Figure 3.6.2*) and then carefully taking the plant from the entire soil but still with the roots attached to the mass of soil. Then soil was gently removed from the plant roots followed by visual observation and measurements. Rooting depth was obtained by measuring the length of the root from the root crown to the tip of the longest root using a ruler (*Figure 3.6.2)*. Rooting width was measured at the widest position of the root from one side to the other side using a ruler (following gentle soil removal by water without disturbing the root orientation/width).

Figure 3.6.2: (A) Excavation of plant for root measurements (B) Plant laid on protractor sheet for angle determination (C) Measuring rooting depth (D) Measuring root angle during the experiment conducted at Naliendele Agricultural Research Institute, Mtwara between July and October 2016.

3.7 Rainout shelter experiments

3.7.1 Soil preparation

A mixture of clay soil and river sand was prepared in a ratio of 1:2 respectively (*Figure 3.7.1)*. The ratio of 1:2 (clay soil:sand) was chosen to mimic the soil textural class in the field experiments in Tanzania. The textural class of the mixed soil was loamy sand. Detailed physical and chemical properties of the soil are found in *Table 5.3.1.*

Figure 3.7.1: Soil preparation for seed sowing in a rainout shelter at University of Nottingham Malaysia in 2018 season.

Soil packing into PVC columns

The amount of soil packed to the PVC columns depended on: bulk density of the loamy sand which ranges between 1.5 – 1.75 g cm^{-3} (Morris and Lowery, 1988; Cresswell and Hamilton 2002) and the volume of the PVC columns. Basing on soil textural class, loamy sand (*Table 5.3.1)*, the bulk density of 1.6 g cm^{-3} was optimized. Calculation of amount of soil for each PVC column followed the equation adopted from Cresswell and Hamilton (2002).

$$Dry\ soil\ weight\ (g) = (Bulk\ density\ (g\ cm^{-3}) * (Soil\ volume\ (cm^3))$$ .....*Equation 2*

3.7.2 Experimental layout

During the course of the two rainout shelter experiments, (2016/2017 and 2017/2018 cropping seasons) the following protocol was followed. Phenyl vinyl chloride (PVC) columns were used to grow bambara groundnut and groundnut plants under well-watered and water deficit conditions. The design used was adopted from Asch et al. (2005). PVC columns of 0.2

m in diameter and 1 m high were used. The columns were arranged in four blocks while treatments were replicated thrice. Each replication contained 48 columns with 12 treatments in combination. Plants were randomly assigned into one of the three water regimes: well-watered, water withheld during flowering and water withheld during pod development. The columns were supported by hard wooden frames to avoid falling (*Figure 3.7.2)*. Each column weighed about 50 kg of sand: clay soil mixture. Before sowing, soil moisture at field capacity (FC) was determined (13%) as a basis for controlling the amount of water to be irrigated. For determination of soil moisture at FC, the columns with soil were saturated with water then left overnight followed by determinantion of available soil moisture volume by volume.

Soil moisture content in the column was monitored using a PR2 theta probe (Delta T Devices, UK, 1971) for compensation of moisture loss while maintaining the amount of soil moisture in respective treatments. The columns were irrigated manually to ensure the amount of moisture loss is replenished.

Figure 3.7.2: Experimental layout in the rainout shelter at University of Nottingham Malaysia during 2018 season.

3.7.3 Cultural practices

A mixture of clay soil and river sand was put in phenyl vinyl chloride (PVC) columns followed by thorough compaction. Each column contained 50 kg of the mixed soil. Before sowing, soil moisture at field capacity was determined as a basis for controlling the amount of water to be irrigated. The soil-filled columns were saturated with water and left overnight. After that, the soil moisture at field capacity was measured using PR2 theta probe (Delta T Devices, UK, 1971).

Seeds were soaked in water overnight before being sown. Direct sowing of four seeds per column was done at a depth of 3 cm using dibbling method. Thinning to one seedling per column was done ten days after sowing. Before imposing water stress, all plants were well watered regularly until the start of flowering. Irrigation was done manually using a measuring cylinder to ensure the same amount of moisture loss was replenished. Each column was supplied with 500 ml at early stages of growth and later on increased up to 1000 ml depending on landrace water usage and growth stage. The PR2 soil moisture Theta Probe was used to monitor the Soil moisture content. Measurements were done on weekly basis at 30 cm, 60 cm and 90 cm depths in one specific column per every plot.

Fertilizer was applied at the rate of 20:60:40 kg ha^{-1} for nitrogen, phosphorus and potassium (NPK) respectively. NPK were applied in the form of urea [46%, H_2NCONH_2], triple super phosphate [46 % phosphorus pentoxide (P_2O_5)] and muriate of potash [60 % potassium oxide (K_2O)] respectively. The quantity of N, P and K applied was calculated from their respective compounds. Similarly, amount applied per plant was converted from the amount required per hectare. P and K fertilizers were applied and incorporated into the soil at sowing whereas N was applied two weeks after emergency. A mixture of fungicide (Mancozeb 80 % w/w at the

rate of 2.5 g l^{-1} of water) and insecticide (Cypermethrin 5.5 % at the rate of 2.5 ml l^{-1} of water) was sprayed at the start of flowering, then followed by two sprays in two weeks interval (3, 5 and 7 weeks after emergence) for the control of diseases and insects. Plant harvesting was done manually at physiological maturity, when the leaves turned yellow and the parenchymatous layer within the pods had disappeared, using a hand and a hand fork. The harvested pods were threshed and air-dried in the rainout shelter. Later on, the pods containing seeds were further dried in the oven at 40^{o}C for 72 hours (Saddique et al., 2003). After shelling of pods, yield parameters like shelling percentage, 100 seed weight, pod yield per plant, grain yield per plant were calculated accordingly.

3.7.4 Data collection

3.7.4.1 Gas exchange measurements

Photosynthesis rate, stomatal conductance to water vapour, intra cellular Carbon and transpirational rate were measured on the youngest fully expanded leaf using a Li-6400 photosynthesis system (Li-Cor Biosciences, Lincoln, NE, USA) (*Figure 3.7.3*). Two leaves per plant were used for replicate measurements. Measurements were done between 0900 - 1100 hrs at PAR of 500 mol m^{-2} s^{-1}, a reference CO_2 concentration of 380 mmol mol^{-1} and sample relative humidity at 60%.

Figure 3.7.3: Gases exchange measurements in one of the experiments conducted in the rain out shelter at University of Nottingham Malaysia in 2017.

3.7.4.2 Free proline concentration

Proline (symbol Pro or P) is a proteinogenic amino acid that is used in the biosynthesis of proteins and is associated with cell osmotic adjustment and protection (Zhang et al., 2009). Accumulation of proline in plant leaves is a common response of plants to drought stress (Vurayai et al, 2011a; Tsoata et al., 2015). During the course of the experiments, free proline content was measured to assess the response of bambara groundnut and groundnut to drought stress.

Proline content was determined according to the method by Bates et al. (1973). Leaf samples from youngest full-expanded leaves were harvested, put in aluminium foil paper and frozen in liquid nitrogen, before being taken off and stored in -80^{o}C freezer. Later on, the samples were ground into fine powder under liquid nitrogen using mortar and pestle. Subsequently, 0.5 g of ground leaf material was homogenized in 10 ml of 3% aqueous sulphosalicyclic acid (SA). Samples were then centrifuged for 5 minutes at room temperature at a speed of 10,000

rpm. Two ml of the filtrate/supernatant was added to a test tube containing reaction mixture (1 ml 0f 3% SA, 2 ml of glacial acetic acid and 2 ml acid ninhydrin). The solution was then heated in a boiling (96°C) water bath for 60 minutes. The reaction was then terminated in an ice water bath. The reaction mixture was extracted with 4 ml toluene and vortexed for 15 – 20 sec. The chromosphere containing toluene was aspirated from the aqueous phase, warmed to room temperature and absorbance was read at 520 nm (Biochrom Libra, Cambridge, UK) using toluene as a blank. The proline concentration in the samples was obtained from a standard curve obtained by linear regression of the absorbance of standards with the concentrations. Proline in micromole per gram of leaf fresh weight was calculated using the equation below:

$$Proline\ in\ \mu mole\ g^{-1}\ tissue = \frac{[(\mu g\ proline/ml) * ml\ toluene * ml\ salycylic\ acid\ ]}{(11.5\ \mu mole * sample\ (g))} \text{.....} Equation\ 3$$

Where*:* 115.5 is the molecular weight of proline.

3.7.4.3 Root traits

Roots were carefully extracted from the PVC columns (using water) one by one, placed inside a tray filled with water and washed by hand to remove soil and other debris (*Figure 3.7.4*). Afterwards, to preserve the roots, they were placed inside Ziploc bags and placed in a refrigerator for later analysis. Root samples were scanned in greyscale at 400 dpi using a desktop scanner (Epson Perfection V700, Long Beach, CA, USA). Root images were analysed using WinRhizo Pro software (v2009, Regent Instruments, Montreal, QC, Canada). Several root traits; total length (TL), surface area (SA), average diameter (AD) and average volume (AV) were recorded and analysed (*Figure 3.7.4*).

Figure 3.7.4: Extraction of roots from the PVC columns; 1-plants in PVC columns, 2- opening the column, 3-soil removal by water, 4-debris and soil removal, 5-appreciating the rooting depth, 6- more cleaning and debris removal, 7-suspending the roots in the Plexiglas trays ready for scanning, 8- scanner machine and 9- computer with WinRhizo Pro software.

3.7.4.4 Water Use Efficiency (WUE)

WUE is the yield of harvested products attained from water supplied to the crop (Blum 2005). Agronomic WUE (Jones, 1993) was used to calculate the water use efficiency between treatments.

$$WUE = \frac{GY}{V} \qquad \text{.....Equation 4}$$

Where: WUE = water use efficiency, GY = grain yield and V = total amount of water used in the season.

3.8 Statistical Analysis

The data obtained from field and rainout shelter experiments and laboratory analyses were appropriately analysed statistically using Genstat statistical software version 18 (VSN International Ltd., Hemel Hempstead, UK). Analysis of variance (ANOVA) was carried out to ascertain statistical differences between treatments. In order to avoid the differences that might be caused by species differences, bambara groundnut and groundnut were analysed separately. Multiple comparisons were carried out when necessary using Duncan's Multiple Range Test at 5% level of significance.

CHAPTER FOUR

Response of Bambara Groundnut (*Vigna subterranea* (L.) Verdc) and Groundnut (*Arachis hypogaea* (L.)) to Water Deficit Stress under Field Conditions

4.1 Introduction

According to the United Nation (UN) World Population Prospects (2017), world population is expected to reach 8.6 billion in 2030, 9.8 billion in 2050 and 11.2 billion in 2100. Water scarcity, other effects of climate change and increasing world population paint a gloomy picture of future food security (Chivenge et al., 2015; Stagnari et al., 2017). Water deficit is predicted to become an increasing problem under future climates (Lobell et al., 2011; AghaKouchak et al., 2015; Mehran et al., 2017). Some plants have evolved an array of morphological, physiological, and biochemical adaptations with the aim of escaping, avoiding or tolerating water deficit problems (Basu et al., 2016; Mayes et al., [Submitted]). Limited water for crop production has led to the emergence of previously neglected and underutilized crops (NUCS), such as bambara groundnut (*Vigna subterranea* (L.) Verdc), as possible future crops (Mabhaudhi, 2009). Regardless of negligence from scientific community, NUCS have survived over years often under unfavourable conditions. Underutilized crop species may have evolved to become adapted to adverse conditions such as water deficit stress (Mabhaudhi and Modi, 2015; Mayes et al., [Submitted]). NUCS have a role to play in guaranteeing future food security either directly as alternative crops in areas that are predicted to become drought-prone or indirectly as germplasm resources for crop improvement.

Drought affects crop growth and physiological processes at any developmental stage; while the early reproductive stage is found to be one of the most susceptible phases of a crop to drought stress (Liu et al., 2003; Admasu et al., 2019). Relative water content (RWC), chlorophyll content and stomatal conductance are some of traits that have been used to study drought in plants (Vurayai et al., 2011a; Mabhaudhi and Modi, 2013). Stomatal closure results in decreased diffusion and fixation of carbon dioxide (CO_2) and reduction in photosynthesis. Understanding RWC under low soil moisture is of importance due to the fact that, high RWC appears to be a common trait in drought resistant species (Saraswathi and Paliwal, 2011). Plant species which exhibit restricted changes in RWC per unit reduction in water potential, are often considered relatively drought resistant (Painawadee et al., 2009). Plants fall under the drought resistant category because of their ability to conserve leaf available water under water stress conditions. This is achieved either by maximizing water uptake and stomatal closure e.g. cowpeas *(Vigna unguiculata* (L.) Walp.) and sorghum *(Sorghum bicolor* (L.) Moench) (drought avoidance) (Ludlow, 1989) or by maximizing water uptake and osmotic adjustment which enhances turgor maintenance, allowing stomatal opening, photosynthesis and leaf expansion to be maintained over a wider range of soil moisture stress e.g. groundnut (*Arachis hypogaea* L.), pigeonpea *(Cajanus cajan* (L.) Millspaugh) and cotton *(Gossypium hirsutum)* (dehydration tolerance) (Collinson et al., 1997).

Bambara groundnut is the third most important legume after groundnut and cowpea (*Vigna unguiculata*) (Basu et al., 2007). Smallholder farmers in tropical and subtropical countries in sub-Saharan Africa and some parts of Latin America and Asia cultivate it (Linnemann and Azam-Ali, 1993; Bamshaiye et al., 2011) thus considered as famine crop. Famine crop because of its high nutritional value, drought resistance and the ability to produce in soils considered

insufficiently fertile for cultivation of other more favoured species (Azam-Ali et al., 2001). However, despite its importance, bambara groundnut is still cultivated from local landraces and hence farm yields are still very low (Hillocks et al., 2012; Chibarabada et al., 2015).

Bambara groundnut has widely been reported as drought resistant (Linnemann et al., 1993; Mwale et al., 2007a; Vurayai et al., 2011a; Mabhaudhi et al., 2013; Mabhaudhi and Modi, 2013). Understanding its response to water deficit is important for future crop improvement. Therefore, the objective of this study was to determine the response of bambara groundnut and groundnut *(Arachis hypogaea* (L.)) (as a comparator crop) to water deficit stress imposed at different growth stages under field conditions.

4.2 Field experiment 1: The response of bambara groundnut landraces and groundnut to water deficit stress

4.2.1 Materials and methods

4.2.1.1 Experimental site and treatments

The description for the experimental is presented in chapter 3 under section 3.2. Test crops involved two bambara groundnut landraces (NALBAM 2 and NALBAM 4) and one groundnut variety (MNANJE). For more details see section 3.3.1. Water supply treatments are described in chapter 3 section 3.3.2.

4.2.1.2 Cultural practices

The experiment was conducted from July to November 2016 at Naliendele Agricultural Research Institute experimental sites in Mtwara, Tanzania. Details for the experimental site are presented in chapter 3 section 3.2. Neither fertilizers nor herbicides were applied to the

plants during the experiment. For other cultural activities like weeding and water application, see chapter 3 section 3.6.2.

4.2.1.3 Data collection and analysis

Most data collected under this experiment were common to other experiments and therefore described under chapter 3. These includes growth data, relative water content, leaf chlorophyll content index (under section 3.5), stomatal conductance, and root architecture (under section 3.6.3).

Soil Data

Results for soil characterization and methods used are presents in table (Field soil moisture content was monitored by gravimetric soil moisture determination method. Gravimetric soil water content (θg) is the mass of water per mass of dry soil. Moist soil samples were taken using cores, weighed, oven dried at 105°C for 48 h and then reweighed. Then, gravimetric soil moisture content was calculated by taking the mass of water lost as a percentage of the mass of the dried soil (Black, 1965).

$$\theta_g(\%) = \left(\frac{\text{weight of wet soil} - \text{weight of dry soil}}{\text{weight of dry soil}}\right) * 100 \quad \text{.....Equation 5}$$

Where: θg = gravimetric water content.

Environmental data

Weather conditions during the experiment were recorded at the Naliendele Agricultural Research Institute (NARI) weather station and are presented in *Figure 4.2.1* and *Figure 4.2.2*. The station is located about 1000 m from the experimental site.

4.2.2 Results

4.2.2.1 Environmental conditions

The experiment was conducted during the dry season, June – November 2016. Observations for rainfall (mm), temperatures (°C), percentage relative humidity (%), pan evaporation (mm) and sunshine (hour) are presented in *Figure 4.2.1* and *Figure 4.2.2.*

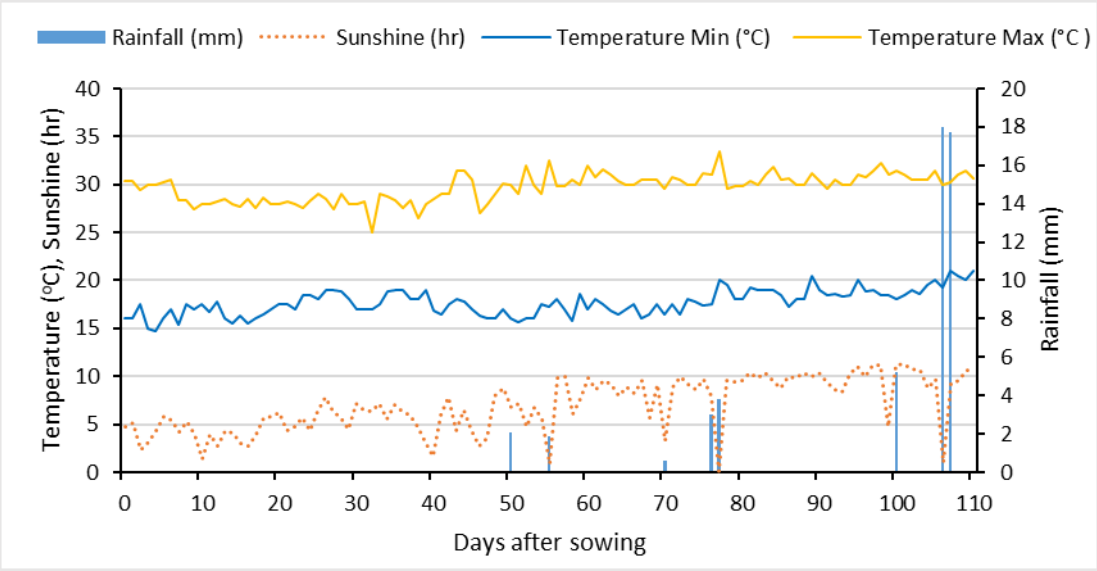


Figure 4.2.1: Temperature (max °C and min °C), rainfall (mm) and sunshine (hr) during the experiment conducted at Naliendele Agricultural Research Institute, Mtwara between July and November 2016.

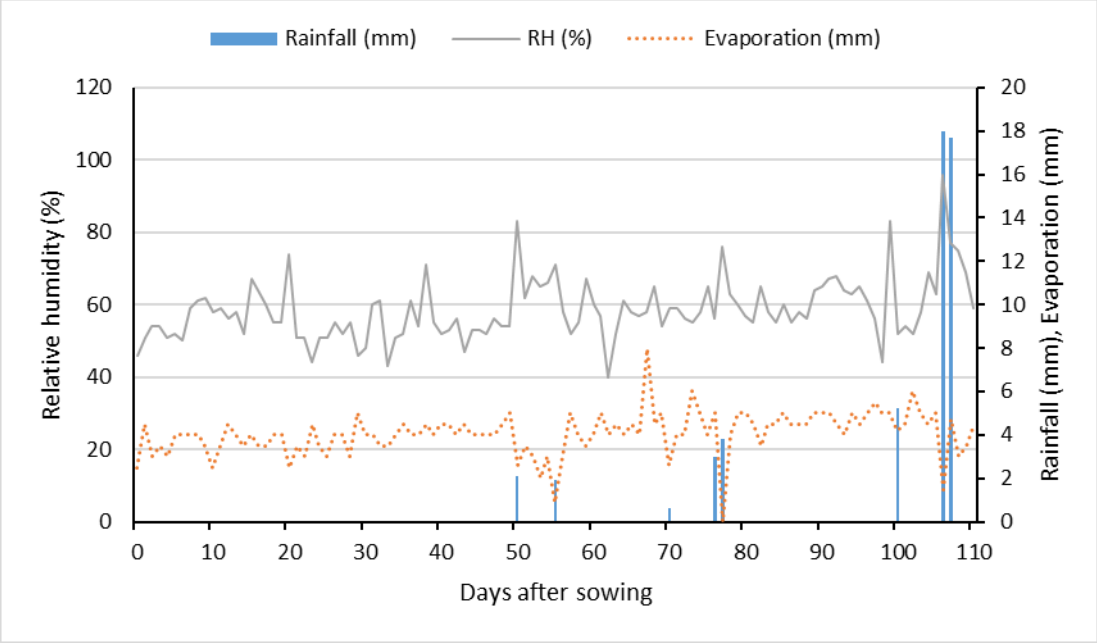


Figure 4.2.2: Relative humidity (RH %), rainfall (mm) and evaporation (mm) during the experiment conducted at Naliendele Agricultural Research Institute, Mtwara between July and November 2016.

4.2.2.2 Effects of water deficit on soil main effects

Water regimes

Figure 4.2.3 shows soil moisture contents of different water regimes at 30 cm depth during the experiment. Soil moisture contents of all water regimes, (control, water deficit stress during flowering and pod development) differed significantly ($p < 0.001$) as plant growth and development progressed. Soil moisture content decreased with plant age under all treatments. Lower values of stored soil moisture content were found during pod development water deficit stress relative to water deficit stress during flowering, although these were not significant. Nevertheless, higher moisture differences between control and water deficit stress plots were revealed during flowering as compared to pod development stage.

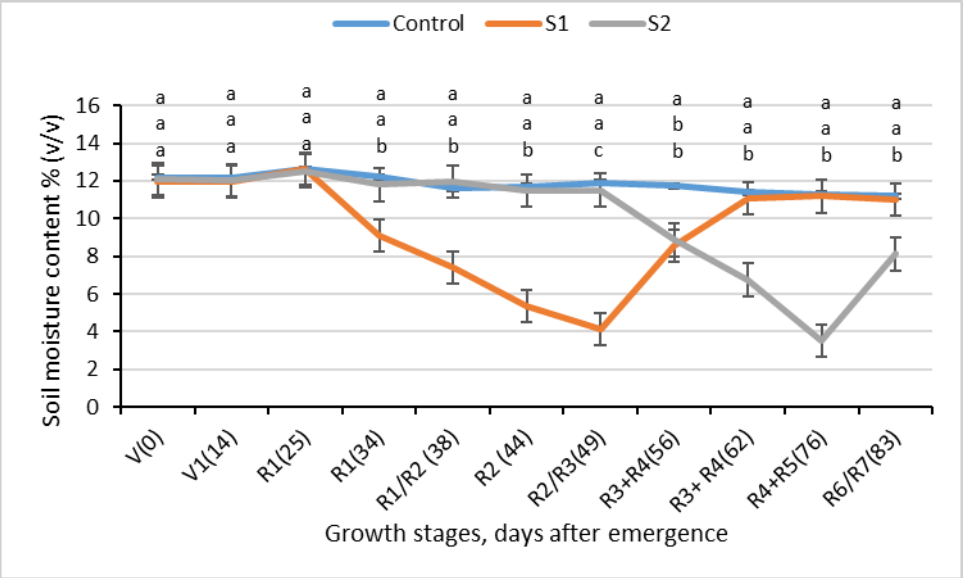


Figure 4.2.3: Water deficit stress on soil moisture content during different growth stages in an experiment conducted at Naliendele Agricultural Research Institute, Tanzania in 2016 dry season. S1 = water deficit stress during flowering, S2 = water deficit stress during pod development, V = vegetative, R1 = Flowering, R2 = beginning peg, R3=beginning pod, R4 =full pod, R5 = beginning seed, R6 = full seed, R7 = beginning maturity (n = 6).

Plant materials

Significant differences ($p < 0.05$) existed among the landraces during both water deficit stress periods (*Figure 4.2.4*). Soil moisture content among bambara groundnut landraces was

consistently lower in NALBAM 2 compared to NALBAM 4. Although groundnut landrace (MNANJE) was analysed separately, it can be clearly seen that, the moisture remaining in the soil in MNANJE is quite low as compared to bambara groundnut landraces. Reduction in soil moisture content was more pronounced during flowering stage as compared to pod development stage (*Figure 4.2.4).*

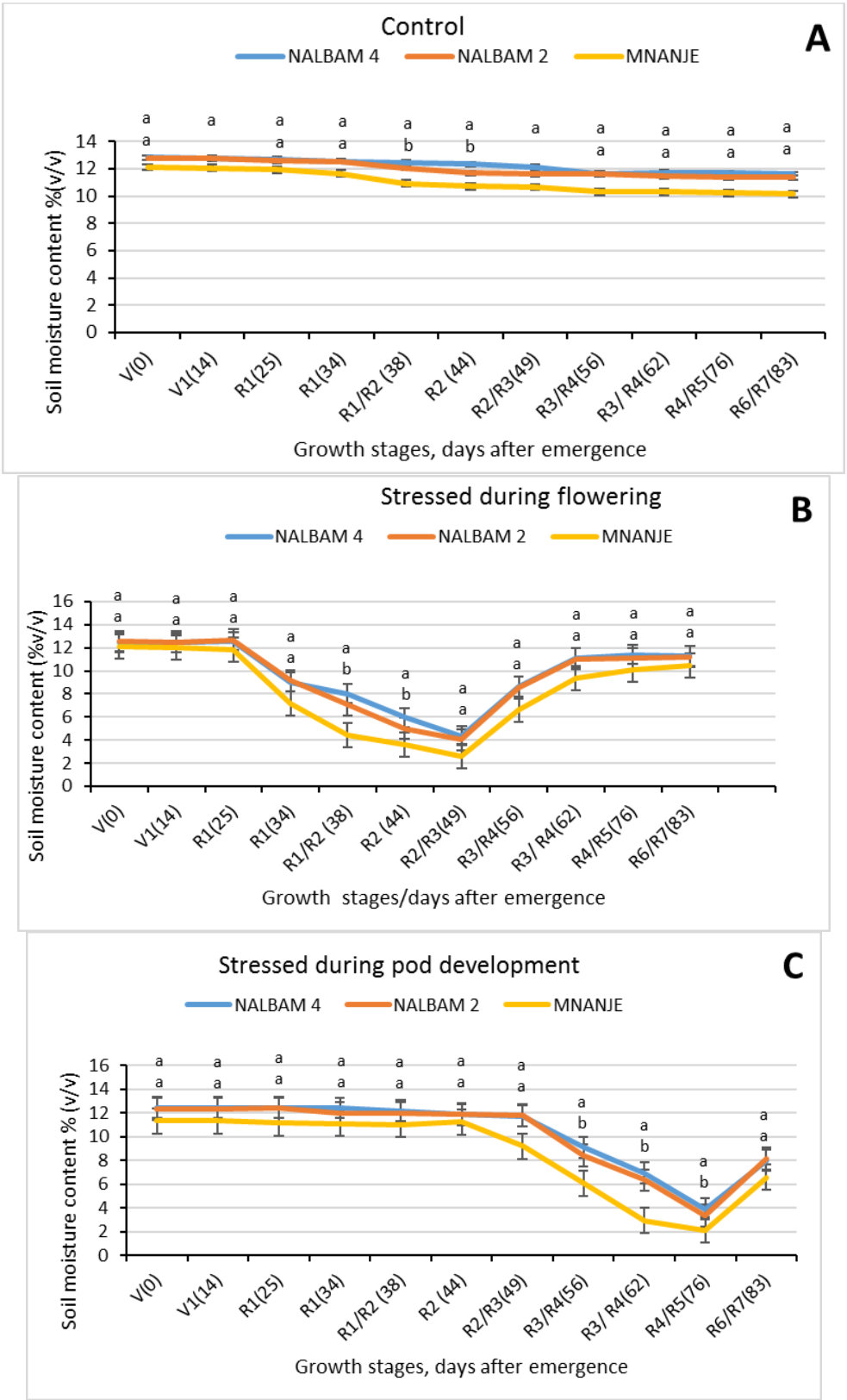


Figure 4.2.4:Variations in soil moisture content in bambara groundnut (NALBAM 4, NALBAM 2) and groundnut (MNANJE) landraces under three water regimes and different developmental stages during the experiment conducted at Naliendele Agricultural Research Institute, Mtwara between July and November 2016; (A) Control, (B) water deficit stress during flowering, (C) water deficit stress during pod development. V = vegetative, R1 = Flowering, R2 = beginning peg, R3=beginning pod, R4 =full pod, R5 = beginning seed, R6 = full seed, R7 = beginning maturity. (n = 6).

4.2.2.3 Above ground traits

Phenological stages

There was no significant ($p > 0.05$) differences observed between the bambara groundnut landraces. Although analysed separately, MNANJE (groundnut) was found to flower and reach physiological maturity earlier as compared to bambara groundnut landraces.

Stomatal conductance

Stomatal conductance decreased in water deficit treatments (*Table 4.2.1*). Significant differences ($p < 0.001$) were found between the control and water deficit stressed plots. The plants that were water stressed during flowering revealed higher reduction percentage values as compared to those stressed during pod development. Stomatal conductance significantly ($p < 0.001$) differed between NALBAM 4 and NALBAM 2, interaction between water regimes and landraces was significant at ($p < 0.01$) during flowering and at ($p < 0.001$) during pod development. NALBAM 4 consistently showed higher stomatal conductance values as well as lower percentage changes than NALBAM 2. Similarly, insufficient water significantly ($p < 0.001$) reduced stomatal conductance in MNANJE (*Table 4.2.1)*. However, highest stomatal conductance values accompanied with lowest percentage reduction in stomatal conductance was expressed by the groundnut (MNANJE) during both water deficit stress periods (*Table 4.2.1).*

Table 4.2.1: Stomatal conductance (mmol m^{-2} s^{-1}) of bambara groundnut (NALBAM 4 and NALBAM 2) and groundnut (MNANJE) landraces grown under control and water deficit conditions during 2016 dry season under field conditions.

Treatments		Stomatal conductance (mmol m^{-2} s^{-1})			
		S1	% Δ	S2	% Δ
Water regimes	Control	306.60[a]		323.40[a]	
	Stressed	103.40[b]	-66	126.20[c]	-61
Landraces	NALBAM 4	256.00[a]		259.90[a]	
	NALBAM 2	233.20[b]		244.60[b]	
	MNANJE	309.13		317.57	
Interaction					
NALBAM 4	Control	294.9[ab]		300.2[a]	
	Stressed	112.5[c]	-62	124.1[d]	-59
NALBAM 2	Control	285[b]		297.3[bc]	
	Stressed	98.3[c]	-66	111.5[e]	-62
Water regimes	p-value	<.001		<.001	
Landraces	p-value	<.001		<.001	
Interaction	p-value	0.01		<.001	
MNANJE	Control	360.20[a]		354.90[a]	
	Stressed	206.80[b]	-43	260.00[b]	-27
	p-value	<.001		<.001	

Means within the same column followed by the same letter are not significantly different at 5% level based on Duncan's Multiple Range Test. % Δ = Percentage change between control and water stressed plants, S1 = water deficit stress during flowering, S2 = water deficit stress during pod development. (n =12)

Chlorophyll content index

Results of chlorophyll content index showed significant differences ($p < 0.001$) between well-watered and water deficit stressed treatments in both bambara groundnut and groundnut. While water deficit stress reduced leaf chlorophyll content index (CCI) in bambara groundnut landraces, on the other hand it increased CCI in groundnut (*Figure 4.2.5*. As it can be observed from *Figure 4.2.5*, higher discrepancies was expressed during flowering stage. Significant ($p < 0.001$) differences existed between the bambara groundnut landraces. Interaction between water regimes and landraces was also significant at ($p < 0.01$). From the current results, NALBAM 2 outweighed NALBAM 4 in CCI values. Higher percentage reduction values were observed in NALBAM 2 as compared to NALBAM 4. MNANJE was superior in CCI values. Highest values of CCI in bambara groundnut was revealed in control plants (NALBAM 2 (51) and NALBAM 4 (47), whereas highest values in MNANJE were observed in water deficit stressed plants (during flowering (54) and during podding (60)) *Figure 4.2.5*).

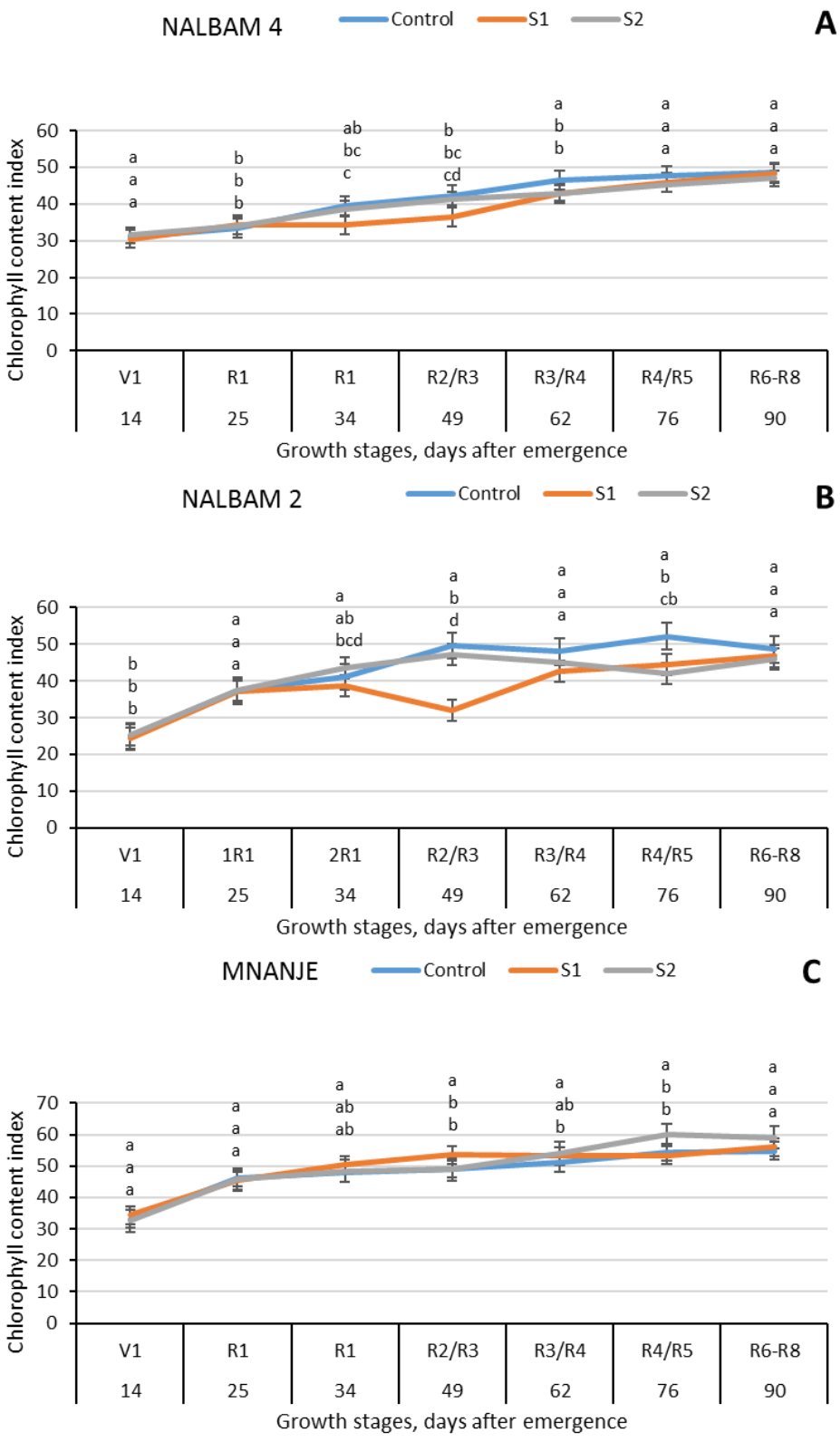


Figure 4.2.5: Water deficit stress on chlorophyll content index of bambara groundnut; (A)NALBAM 4, (B)NALBAM 2 and groundnut (C)MNANJE landraces under well-watered (Control) and water deficit conditions during the 2016 dry season at Naliendele Agricultural Research Institute Mtwara, trial site. S1= water deficit stress during flowering, S2 = water deficit stress during pod development, V = vegetative, R1 = Flowering, R2 = beginning peg, R3 =beginning pod, R4 =full pod, R5 = beginning seed, R6 = full seed, R7 = beginning maturity, R8 = harvest maturity. (n = 18).

Relative leaf water content (RWC)

Results for RWC are presented in *Figure 4.2.6.* Relative water content decreased under water deficit in both bambara groundnut and groundnut. The decrease was significant ($p < 0.001$) in all landraces during flowering and pod development water deficit stress compared with the control. Plants stressed during flowering were more affected as compared to those stressed during pod development. Significant ($p < 0.001$) difference in RWC levels was also observed between bambara groundnut landraces, with the highest values observed in NALBAM 4 during both water deficit stress periods. Percentage changes in RWC during flowering and pod development were smaller in NALBAM 4 as compared to NALBAM 2. MNANJE, the groundnut, had the highest RWC values as compared to bambara groundnut landraces (*Figure 4.2.6)*. Moreover, MNANJE showed the smallest percentage decrease in RWC during both water deficit stressed periods.

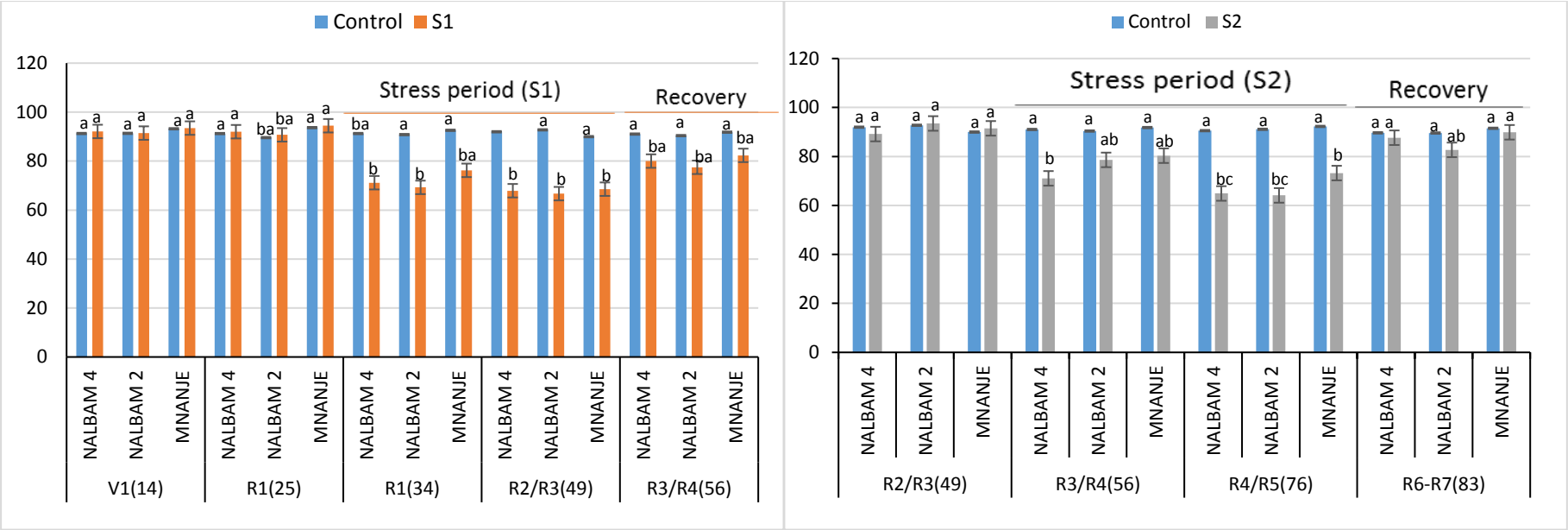


Figure 4.2.6: Relative water content (%) of bambara groundnut (NALBAM 4, NALBAM 2) and groundnut (MNANJE) landraces under well irrigated (Control) and water deficit conditions in field during the 2016 dry season. S1= water deficit stress during flowering, S2 = water deficit stress during pod development, R1 = Flowering, R2 = Beginning peg, R3 =Beginning pod, R4 = Full pod, R5 = Beginning seed R6 = full seed, R7 = beginning maturity. (n = 6).

Plant height

Table 4.2.2 presents results for plant height. Water deficit stress caused significant ($p < 0.05$) differences in landraces height. The changes in plant height between control and water deficit stressed plants were higher during flowering than during pod development stage. Bambara groundnut landraces also differed significantly ($p < 0.05$) during both water deficit stress periods. Similarly, significant differences ($p < 0.001$) existed in the interaction between water regimes and landraces (*Table 4.2.2*). NALBAM 4 outweighed NALBAM 2 in terms of plant height. During flowering, the highest percentage decrease in plant height was observed in NALBAM 2. Plants showed higher plant height values in well-watered plots as compared to plots under water deficit stress. Groundnut (MNANJE) consistently showed lowest percent decrease between control and water deficit stressed plants (*Table 4.2.2*).

Canopy spread

Water deficit stress significantly reduced canopy spread of both bambara groundnut ($p < 0.05$) and groundnut ($p < 0.001$) *(Table 4.2.2*). Significant ($p < 0.001$) differences were observed among bambara groundnut landraces and in interaction between water regimes and landraces only during flowering. The effect of water deficit stress was more pronounced during flowering stage as compared to pod development stage. Among bambara groundnut landraces, NALBAM 4 had wider canopy spread than NALBAM 2. As expected, MNANJE, the groundnut showed the widest canopy spread as compared to bambara groundnut landraces, but with the lowest percentage decrease values in both water deficit stress periods.

Table 4.2.2: Effect of water deficit stress on plant height (cm), canopy spread (cm) and rooting depth (cm) during flowering and pod development stages in 2016 dry season at Naliendele Agricultural Research Institute Mtwara, Tanzania trial site.

Treatments		Plant height				Canopy				Rooting depth			
		S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ
Water regimes	Control	21.39^{a}		23.09^{a}		25.22^{a}		29.10^{a}		23.03^{a}		33.36^{a}	
	Stressed	20.16^{a}	-5.75	21.98^{b}	-4.81	22.69^{b}	-10	26.69^{b}	-8.28	19.89^{b}	-13.6	29.16^{c}	-12.59
	p-value	0.28		0.03		0.037		0.001		0.01		<.001	
Landraces	NALBAM 4	21.18^{a}		21.05^{b}		24.66a		26.91^{a}		26.43^{a}		33.97^{a}	
	NALBAM 2	20.62^{a}		22.40^{a}		23.74^{b}		26.43^{a}		19.67^{b}		27.93^{b}	
	p-value	0.05		0.001		<.001		0.267		<.001		<.001	
	MNANJE	21.85		23.66		26.09		33.57		29.72		38.82	
Interaction													
NALBAM 4	Control	22.8^{a}		24.06^{a}		26.78^{a}		28.94^{a}		28.40^{a}		37.47^{a}	
	Stressed	20.01^{abc}	-12.23	21.98^{c}	-8.6	22.94^{b}	-14.3	26.61^{ab}	-8.05	22.33^{b}	-21.4	32.40^{b}	-13.5
NALBAM 2	Control	20.68^{bcd}		22.56^{ab}		24.94^{b}		29.18^{a}		24.33^{bc}		31.30^{b}	
	Stressed	17.67^{db}	-14.55	20.42^{c}	-9.5	21.16^{c}	-15.2	26.72^{ab}	-8.43	18.67^{c}	-23.26	25.13^{c}	-19.7
Interaction	*p-value*	<.001		<.001		<.001		0.078		0.001		0.31	
MNANJE	Control	23.08^{a}		24.05^{a}		28.13^{a}		34.94^{a}		32.17^{a}		42.67^{a}	
	Stressed	20.61^{b}	-10.7	23.27^{a}	-3.2	24.04^{c}	-14.5	32.17^{b}	-7.9	26.20^{b}	-18.56	37.50^{b}	-12.12
	p-value	<.001		0.23		<.001		<.001		<.001		<.001	

Means within the same column followed by the same letter are not significantly different at 5% level based on Duncan's Multiple Range Test. % Δ = Percentage change between control and water stressed plants, S1 = water deficit stress during flowering, S2 = water deficit stress during pod development. (n =6).

4.2.2.4 Root traits

Rooting depth

Significant ($p < 0.001$) differences in rooting depth existed among water regimes (*Table 4.2.2*). Similarly, rooting depth varied significantly ($p < 0.001$) between the bambara groundnut landraces. The interaction between the two was significant at ($p < 0.001$). Higher values were observed in control plots as compared to water deficit stressed plots. The effect was more pronounced during water deficit stress imposed during flowering than during pod development. NALBAM 4 had deeper rooting and lower percentage decrease in rooting depth during the growing season as compared to NALBAM 2 (*Table 4.2.2*). MNANJE, the groundnut, was superior to both bambara groundnut landraces. MNANJE showed the deepest rooting depths as well as the least percentage changes between control and water deficit stressed plants during both water deficit stress periods (*Table 4.2.2*).

Root width

Water deficit stress reduced root system width significantly ($p = 0.001$) during flowering, while there was no significant changes during pod development (*Table 4.2.3)*. Similarly, bambara groundnut landraces showed significant ($p < 0.001$) differences only during flowering (*Table 4.2.3*). The interaction between watering regimes and bambara groundnut landraces was not significant ($p > 0.05$). Water deficit stress significantly ($p = 0.001$) affected groundnut landrace (MNANJE) during both water deficit stress periods (*Table 4.2.3*). Higher values for rooting width were observed in the well-watered condition than in the water-limited treatments. Plants that were water deficit stressed during flowering exhibited higher percentage decrease compared to the plants water deficit stressed during pod development. NALBAM 4 had higher root spread as compared to NALBAM 2. The percentage reduction in root width shown by

NALBAM 4 and NALBAM 2 were almost similar during flowering, but higher in NALBAM 2 during pod development stage (*Table 4.2.3*). MNANJE showed the widest rooting width as compared to bambara groundnut landraces during both water stress periods. Percentage change between well-watered and water stressed plants during flowering was smallest in MNANJE. On the other hand, MNANJE showed the highest percentage change during pod development water stress as compared to NALBAM 4 and NALABMA 2 (*Table 4.2.3*).

Rooting angle

Water deficit stress did not significantly ($p > 0.05$) affect the rooting angle between the well-watered plots and water stressed plots. Similarly, water deficit stress, neither significantly ($p > 0.05$) changed root angle in the bambara groundnut landraces nor in the groundnut (MNANJE). The interaction between water regimes and landraces was also not significant at ($p > 0.05$). Relatively higher values of root angle were found in well-watered plots than in water deficit stressed plots. Percentage increase in root angle was more pronounced during flowering than during pod development. Between the bambara groundnut landraces, NALBAM 2 had the higher average root angle as compared to NALBAM 4. Nevertheless, NALBAM 4 showed higher percent increase than NALBAM 2. MNANJE had the highest root angle values as compared to bambara groundnut landraces. MNANJE showed the highest percentage increase in root angle during both water deficit stress periods.

Root nodules

Significant differences ($p < 0.05$) were found between the water regimes but not in bambara groundnut landraces (*Table 4.2.3*). The interaction between water regimes and bambara groundnut landraces differed significantly ($p = 0.02$) during podding stage. Higher percentage change values were observed during flowering. Among bambara groundnut landraces,

NALBAM 4 had lower percentage decrease values compared to NALBAM 2. MNANJE was also significantly affected by drought stress during both flowering (p = 0.01) and pod development (p = 0.001) stages. MNANJE experienced the highest number of nodules as compared to bambara groundnut landraces in all water regimes throughout the experiment (*Table 4.2.3*). In addition, lowest percentage change values were observed in MNANJE during the growing season.

Table 4.2.3: Effect of soil moisture deficit on number of nodules and root system width under varying water deficit stress imposed at different growth stages during the experiment conducted at Naliendele Agricultural Research Institute, Mtwara between July and November 2016.

Treatments		Root nodules				Root system width (cm)			
		S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ
Water regimes	Control	14.78^{a}		41.33^{a}		10.77^{a}		11.4^{a}	
	Stressed	8.22^{b}	-44.38	37.89^{b}	-8.32	7.88^{b}	-26.83	10.5^{a}	-7.89
Landraces	NALBAM 4	12.44^{a}		39.56^{a}		9.90^{a}		11.07^{a}	
	NALBAM 2	12.33^{a}		39.78^{a}		9.44^{b}		11.02^{a}	
	MNANJE	18.22		67.11		11.07		12.13	
Interaction									
NALBAM 4	Control	14.67^{a}		41.67^{ab}		10.93^{a}		11.37^{a}	
	Stressed	8.33^{a}	-43.22	37.63^{d}	-9.69	8.00^{d}	-26.83	10.5^{a}	-7.65
NALBAM 2	Control	15^{a}		42.33^{a}		10.43^{bc}		11.47^{a}	
	Stressed	8^{a}	-46.67	38^{cd}	-10.23	7.63^{e}	-26.84	10.5^{a}	-8.46
Water regimes	*p-value*	0.016		0.004		0.001		0.3	
Landraces	*p-value*	0.97		0.101		<.001		0.947	
Interaction	*p-value*	0.972		0.022		0.349		0.88	
MNANJE	Control	21^{a}		72.33^{a}		12.03^{a}		12.67^{a}	
	Stressed	13^{b}	-38.10	66.33^{b}	-8.29	9.20^{b}	-23.52	11.13^{b}	-12.15
	p-value	0.01		<.001		0.001		0.001	

Means within the same column followed by the same letter are not significantly different at 5% level based on Duncan's Multiple Range Test. % Δ = Percentage change between control and water stressed plants, S1 = water deficit stress during flowering, S2 = water deficit stress during pod development. (n = 6).

4.2.3 Discussion

Environmental conditions

The trial was conducted during the dry season and very little rainfall (a total of 52.3 mm) was received during the trial period. Drought is mostly assessed in relation to precipitation, degree of dryness and the duration of the dry period. Rainfall, evaporation and solar radiation are the

key factors in this context. Although field drought experiments are difficult to conduct, the data are more reliable as compared to data from controlled environments. The data during the experiment depicted the real conditions associated with low soil moisture. From the current results, out of 110 days of the growing season only 4 days experienced rainfall. In South-eastern Tanzania this is a normal rainfall distribution pattern since the area is under unimodal type of rainfall. Normally the rainfall in the area starts at the end of December and ends in May/June.

Soil moisture content and landraces

Soil water content in control plots consistently decreased with plant growth. These results are in agreement with findings by Ibraheem et al. (2014) who found decrease in stored soil moisture with plant growth. Similarly, soil moisture under water deficit stress plots decreased due to both plant growth and water deficit stress (*Figure 2.5.1*) and was more pronounced during flowering water deficit stress. This trend is reflected in the moisture storage of the soils where water deficit during pod development had the lowest volume of water stored compared with water deficit during flowering. As it can be observed in *Figure 4.2.3*, control plots during flowering had more soil moisture content as compared to control plots during pod development. This implies that, the effect of water deficit became more prominent with progressive plant growth. The differences observed in stored soil moisture under different water regimes between NALBAM 2 and NALBAM 4 is negligible (*Figure 4.2.4*). The higher amount of stored soil moisture in both bambara groundnut landraces can be related to poor acquisition of soil water as both were found to have shallow roots. On the hand, MNANJE (the groundnut) showed the least amount of soil moisture stored in the soil under all water treatments (*Figure 4.2.4*). This implies that, in plants with lower stored soil moisture content, much of the moisture has been taken up by the corresponding landrace/species and hence

high water demand; and vice versa is true. High level of water demand by soybean *(Glycine max* (L.) Merr.) (Pejic et al., 2011), common bean *(Phaseolus Vulgaris L*.) (Carvalho et al., 2016) and chickpea (*Cicer arietinum*) *(*Pang et al., 2017) at reproductive stage has been reported. The reason for low soil moisture storage under all treatments found in MNANJE (*Figure 4.2.4*) may be explained by higher MNANJE shoot biomass, rooting depth and width and subsequently high demand for water. Zougmoré et al. (2004) observed a similar result in organic material treated plots, which had less moisture stored due to more evapotranspirative demand of the more vigorous crops. MNANJE has both vigorous shoot and root growth as compared to bambara groundnut.

Phenological stages

Plant phenology is affected by water deficit in many crops. Collinson et al. (1999) found a reduction in flower production due to drought and Mwale et al. (2007a) reported reduction in pod numbers in bambara groundnut due to drought. Drought escape is a classical adaptive mechanism, which involves rapid plant development to enable the completion of the full life cycle prior to a coming drought event (Shavrukov et al., 2017). According to Araus et al. (2002), flowering is an important adaptation related to drought escape. In groundnut for example, under insufficient water supply, only the first initiated flowers effectively result in pods that contribute to yield (Nageswara Rao et al., 1988). From this study, MNANJE took the least days in attaining all developmental stages. Furthermore, it took fewer days than the two bambara groundnut landraces to reach physiological maturity. This implies that, MNANJE is an early maturing landrace and can adapt to water deficit conditions by drought escape mechanism. NALBAM 4 and NALBAM 2 took longer duration to attain flowering and physiological maturity and therefore can be termed as late maturing bambara groundnut landraces. The current findings in NALBAM 4 and NALBAM 2 can be related to findings by Shumba-Mnyulwa, 2002,

who termed Zebra coloured and Mottled bambara groundnut landrace, which took about 89 days to maturity as early maturing and Burkina bambara groundnut landrace, which took 113 days to maturity was termed as moderate maturing**.** It must be noted that, some landraces are genetically early maturing, while others are not, but when under water deficit stress may mature early. This was not the case for DodR or NALBAM 4. S19-3 and MNANJE probably are genetically early maturing and therefore when grown in drought prone areas may even mature earlier than normal. It can therefore be suggested that, some of the bambara groundnut and groundnut landraces/genotypes can give yields under drought as they are capable of maturing earlier before the drought becomes terminal.

Stomatal conductance

In the current study, under well-watered conditions, both early and late growth stages of plant growth revealed lower stomatal conductance as compared to stomatal conductance at mid growth stages. This suggests that stomatal conductance is affected not only by water deficit stress but also by the age of plants. The current results agree with findings by Karikari et al. (2004), Echer and Rosolem (2015). The study also revealed decreased stomatal conductance with imposition of water deficit stress. Collinson et al. (1997), Cornellisen (2005) and Vurayai et al. (2011b), reported similar results in bambara groundnut. Under well-watered conditions, among bambara groundnut landraces, higher stomatal conductance values were observed in NALBAM 4 than in NALBAM 2. The smallest percentage reduction values in stomatal conductance in both water deficit periods were found in MNANJE. Although, NALBAM 4 showed relatively smaller percentage reduction in stomatal conductance than NALBAM 2 under water deficit conditions, both had higher percentage reductions than MNANJE (*Table 4.2.1*). This indicates low transpiration water use of the two bambara groundnut landraces and higher transpiration water use in MNANJE. Stomatal conductance is closely related to

water status in the soil (Hoshika et al., 2013). In the present study, it was found that water deficit stress decreased stomatal conductance (*Table 4.2.1*), which agrees with the study by Nageswara Rao et al. (1988) and Jongrungklang et al. (2012) who reported decreased transpiration due to water deficit stress. Stomatal closure is a plant's initial response to declining soil water content and has been characterised as a drought avoidance mechanism (Farooq et al., 2009), as well as being a characteristic of increased water use efficiency under drought stress (Blum, 2005, 2009). With respect to the current investigation, NALBAM 2 and NALBAM 4 showed low transpiration rates, because of stomatal closure, while MNANJE expressed higher transpiration rates. Higher transpiration rates shown by MNANJE under water deficit conditions may be related to its ability to extract water in deeper horizons (Chapter 4 and 6) and partly by accumulation of proline (Chapter 5). This implies that MNANJE had the highest ability to photosynthesise and hence better chances of higher yields under water deficit conditions.

Chlorophyll content index

The decrease in chlorophyll content during the pod filling was revealed by both bambara groundnut landraces, but more pronounced in NALBAM 2. Vurayai et al. (2011b) and Cornellisen, (2005) reported non-significant difference in chlorophyll content on bambara groundnut. Nevertheless, Vurayai et al. (2011b) found that, the resistant bambara groundnut landraces were able to maintain chlorophyll content between control and water deficit stressed plants than the drought sensitive bambara groundnut landraces. The decrease in chlorophyll content in the current experiment may be due to the fact that, chlorophyll tends to decline rapidly during leaf senescence (Merzlyak et al., 1999).

During podding stage some leaves were senescing; probably because most of photosynthate were transported to parts with high demand like pods. In addition, the decrease in CCI in bambara groundnut landraces may be attributed to an increase in the activity of chlorophyllase, an enzyme responsible for the breakdown of chlorophyll, which increases with water deficit (Muhammad and Massawe, 2015). Contrary to bambara groundnut landraces, the increase in CCI with imposition of water deficit found in MNANJE (*Figure 4.2.5*), agrees with findings by Arunyanark et al. (2009) and Mamadou et al. (2016) who found increase in CCI in groundnut under water deficit conditions.

This trait can be considered a line of defence against water deficit stress, which can result in drought resistance. The ability to maintain chlorophyll content under drought stress has been suggested as a drought resistance mechanism in groundnut (Savita et al., 2014). The increase of CCI in groundnut under water limiting conditions and as this trait is related to photosynthetic capacity, could be attributed to drought resistance. This is related to groundnut having more photosynthetic machinery per unit leaf area and hence greater assimilation under drought stress (Songsri et al., 2009). Drought resistant groundnut genotypes maintain their leaf water content and increase thickness of the leaves and chlorophyll density at early stage drought condition (Mamadou et al., 2016), this could be the case for MNANJE. With this regard, chlorophyll content index, can be included in traits targeted for screening crops for drought resistance.

Relative water content

Decrease in leaf water content observed in this research (*Figure 4.2.6*) may have been caused by water loss through evapotranspiration and decreased water absorption by the roots when

the soil moisture was insufficient (Chaves et al., 2003). Maintaining high RWC under water stress conditions might be one indicator for drought resistance (Nautiyal et al., 2002).

In this study, bambara groundnut landraces showed high variability in RWC between the control and water stressed plants. MNANJE, the groundnut, maintained relatively higher RWC between the water regimes (*Figure 4.2.6*). According to Stirling et al. (1989), the leaf water status of groundnut showed diurnal variations and osmotic adjustment in expanding leaves. Similar changes were observed in the current findings, where by MNANJE expressed changes in leaf orientations and rolling during the day. This allowed groundnut to maintain higher turgor levels during period of severe stress. The condition rapidly disappeared after re-watering. Surprisingly, although MNANJE showed pronounced signs of wilting under deficit conditions compared to bambara groundnut landraces, it had higher stomatal conductance as compared to bambara groundnut landraces. The higher RWC in MNANJE may be due to its higher osmotic adjustment (Izanloo et al. 2008), as groundnut accumulates high proline content.

Moreover, higher values of RWC in MNANJE might be due to other responses such as leaf rolling, turning/bending away from sunlight and partial senescence of the leaf under water-limited conditions, which was shown by MNANJE. Leaf rolling and partial senescence is related to minimising transpiration losses by direct reducing surface area available for transpiration (Mabhaudhi, 2012). Rolling of leaves has also been reported in maize (Saglam et al., 2014) and Taro (*Colocasia esculenta* l. Schott) (Mabhaudhi, 2012) as a strategy to reduce leaf water loss. The current results suggest that, MNANJE is able to carry out photosynthesis under water scarce conditions and thus important in arid and semi-arid environments.

Plant height and canopy spread

The canopy spread and plant height in both bambara groundnut and groundnut landraces were affected by water deficit stress (*Table 4.2.2*). Similar results were reported by Madukwe et al. (2011) who worked on bambara groundnut, Kalariya et al. (2013) in groundnut and Specht et al. (2001) in soybean. On the other hand, Berchie et al. (2012) reported non-significant differences in bambara groundnut landraces for canopy spread under water deficit and control. The reduction in plant height and canopy spread observed in the current experiment might be associated with decline in cell enlargement and cell growth due to the low turgor pressure under water deficit stress (Liang et al., 2006; Sankar et al., 2014). However, these parameters were observed to be higher in the control plants than in the water deficit stressed plants and could be an indication that the photosynthetic activities per unit leaf area in the control plots were more than that of the plants in the other treatments.

Plants with wider canopies have advantage of utilizing available light for increased photosynthesis. NALBAM 4 appeared to have both greater canopy spread and plant height than NALBAM 2 landrace (*Table 4.2.2*). Although both landraces are bunched types, NALBAM 4 is more vigorous. This has contributed to higher canopy spread and plant height observed in NALBAM 4 than in NALBAM 2. MNANJE, the groundnut, was found to have the widest canopy spread and tallest plant height (*Table 4.2.2)*. The reduction observed in plant height and canopy spread was attributed by reductions of stem and leaf expansion. The small percentage reduction in the two parameters observed during the pod development stage was contributed by the reduced rate of cell division, elongation and development as most of cells had attained maturity (Vurayai et al., 2011a).

Rooting depth

Current findings reveal that, insufficient water supply was more detrimental during flowering. This is contrary to findings by Belachew et al. (2018) who studied drought in faba bean (*Vicia faba* L.) and observed higher percentage decrease in rooting depth during pod development. Across all water regimes, NALBAM2 was found to evidence shallow root depths (*Table 4.2.2*). MNANJE was found to have relatively, deeper roots as compared to NALBAM2 and NALBAM4. This suggests that, MNANJE is capable of exploiting deeper soil horizons for available moisture. Spatial distribution of roots can determine the extent of soil resource acquisition. Since water is more abundant deeper in the soil under drought conditions, plants with deeper roots have a growth advantage under drought (Sponchiado et al., 1989; Ho et al., 2005). Furthermore, it was observed that, deeper roots can extract more water from deeper layers thus avoiding water deficits at critical growth stages resulting in higher biomass (Ludlow and Muchow, 1990).

Rooting depth therefore, can predict the drought resistance of bambara groundnut and groundnut landraces; deep rooted landraces being of advantageous vis shallow rooted ones. The highest rooting depth values found in MNANJE (*Table 4.2.2*) may have been contributed by vigorous growth of MNANJE during early stages. Deeper roots might contribute to water uptake under drought condition, and root systems can mine sufficient water in deep soil horizon for normal transpiration under early season drought (Thangthong et al., 2017).

Rooting width

Groundnut MNANJE showed the widest root system width, which could lead to better soil exploration and water extraction. Both bambara groundnut and groundnut responded similarly to water deficit stress. Higher percentage reduction values in both crops were found during flowering compared to pod development (*Table 4.2.3)*. This implies that, root system

width is more affected by water deficit stress during flowering as compared to pod development water deficit stress.

The results from this study revealed that, MNANJE (groundnut) differed in root width from individual bambara groundnut landraces, whereby MNANJE showed the widest root system width (*Table 4.2.3)*. Other authors have also reported reductions in root system width. Belachew et al. (2018) reported significant reductions in root system width in water deficit stressed faba bean plants as compared to controls. The reduced width of plants under water stress is partly contributed by reduced growth of lateral roots as a result of suppression of the activation of the lateral root meristems (Deak et al., 2005). The reduced root system width observed in the current study might have been contributed to by reduced production of lateral roots under insufficient water supply. Belachew et al. (2018) reported reduced length of laterals and second order of lateral roots due to the imposition of water stress. Other studies also agree with current findings. For example, the rooting width of sorghum (*Sorghum bicolor* Moench) under water deficit stress was reduced due to hindrance of root laterals (Pardales and Kono, 1990) and in chickpeas (Krishnamurthy et al., 1994).

Well-developed roots, (deep root systems and wider laterally distributed) have been considered as an advantage in avoiding drought (Belachew et al., 2018). Other studies have revealed that, prolific and deep rooted accessions showed drought avoidance mechanisms in cowpea (Matsui and Singh, 2003), (Kashiwagi et al., 2005), field pea (*Pisum sativum* L.) and soybean (*Glycine max* (L.) Merr.) (Benjamin and Nielsen, 2006). Hence, crops with a larger root system probably avoid drought through increased access to water in the soil by increased root system width, longer taproot and overall root system.

Root angle

There was no significant differences among the treatments and between their interaction. Studies of root angle have been reported in different crops. For example, Fenta et al. (2014) studied the effect of drought in soybean varieties on root angle, and revealed that, drought did not significantly ($p > 0.05$) change root angle. Root angle is known to affect rooting depth and hence soil water extraction (Araki et al., 2002). Root angle determines the direction of horizontal and vertical distribution of roots in the soil. It is recognized as an essential trait for drought avoidance in sorghum **(**Mace et al., 2012), wheat (*Triticum aestivum*) (Christopher et al., 2013), and rice (*Oryza sativa*) (Uga et al., 2013; 2015). Studies on drought in upland rice done by Uga et al. (2015) demonstrates that the larger root growth angle (RGA) contributes to avoiding drought stress and consequently higher yield.

In the present experiment, plants stressed during flowering had higher root angle percentage increase values as compared to plants stressed during pod development. This suggests that water deficit stress during flowering is more sensitive than water deficit stress during pod development. Different reports have shown that, plants with wider root angle also had increased rooting depth; in rice (Kato et al., 2006), chickpea (Sayar et al., 2007; Kashiwagi et al., 2015), and sorghum (Singh et al., 2011). Wider root angles could reduce the energy inputs to penetrate in deeper horizons to access water during limited rainfall (Wasson et al., 2012; Meister et al., 2014). MNANJE having the widest root angle as compared to bambara groundnut landraces, it can be considered as drought resistant through its ability to penetrate deeper soil horizons to access available water.

Root nodules

Hsiao and Xu (2000) reported that a reduction in soil water content can adversely affect root hair and retard nodule growth and nitrogen fixation. In an investigation by Ramos et al. (2003)

stated that once nodules are formed, water deficit stress could affect morphological and physiological structure and function. The current results reveal that, in well-watered plots, number of nodules increased progressively both in bambara groundnut and groundnut (*Table 4.2.3*). This implies that, formation of nodules is partly dependent on availability of soil moisture. Ranawake et al. (2011) in an experiment on mung bean found that nodule number was low in stressed plants as compared to the well-watered ones. The results from a study on bambara groundnut conducted by Madukwe et al. (2011) showed that, the highest number of nodules were obtained from the well-watered plots. Water availability in the soil influences survival and metabolic activity of nitrogen fixing bacteria and plants and their symbiotic interactions (Werner and Newton, 2005). Plant nodules numbers are reduced when plants are subjected to water deficit stress (Márquez-García et al., 2015). Leung and Bottomley (1994) reported that, water deficit stress inhibits growth of rhizobia and nodulation. The low number of nodules observed under water stressed conditions in the present experiment (*Table 4.2.3*), can be associated with the impairment of growth, survival and interaction of nitrogen fixing bacteria which resulted to poor nodules formation and/or growth.

4.2.4 Key observations and findings

The present study revealed that water deficit stress caused a reduction in RWC, stomatal conductance and root traits of both bambara groundnut and groundnut. Insufficient water supply increased chlorophyll content in groundnut but reduced it in bambara groundnut landraces. The extent of damage and the ability of the studied crops to withstand water stress depends on the developmental stage at which the plant was exposed to water deficit. Bambara groundnut and groundnut plants are most sensitive to water stress during flowering compared to pod development stage. Bambara groundnut landraces demonstrated drought

avoidance mechanisms, whereas groundnut showed both drought avoidance and escape mechanisms. Drought avoidance was achieved by minimising water losses through stomatal closure. On the other hand, the drought escape mechanism shown by MNANJE was achieved by early maturity. MNANJE groundnut showed better resilience to water deficit stress and the weather experienced during the experiment. Bambara groundnut landraces, NALBAM 4 and NALBAM 2 were affected by the prevailing weather conditions which led to drying of leaves and death of most of plants. This was believed to be associated with low temperatures experienced during the season, where bambara groundnut either failed completely or gave negligible yield. It is recommended that, more research should be done both on water deficit stress and temperature with various bambara groundnut and groundnut landraces for comparison. It is important that comparisons of landraces and species are done over a number of seasons and in different sites in order to further investigate the effect of temperature on crop yield.

The failure of bambara groundnut landraces to perform better during 2016 dry season experiment, called for more experiments. Similar experiment was proposed and conducted in the following dry season (July – November 2017) under field conditions, which involved three bambara groundnut landraces and one groundnut landrace in two sites. Furthermore, similar experiments were conducted under rainout shelter conditions in two consecutive seasons (March – July 2017 and March – July 2018). The study was not only to investigate/avoid the reasons behind the poor performance of bambara groundnut faced in the first field condition experiment but also to explore both physiological and root traits related to drought stress.

4.3 Field experiments two and three: The response of bambara groundnut landraces and groundnut to water deficit stress

4.3.1 Materials and Methods

4.3.1.1 Experimental site and plant materials

Description of the experimental site is presented in section 3.2. Test crops used were three bambara groundnut landraces (DodR, NALBAM 4, S19-3) and one groundnut landrace (MNANJE). For details of the landraces see section 3.3.1. NALBAM 2 was not included to successive experiments following its very poor survive during the field experiment in 2016.

4.3.1.2 Weather data and soil characteristics

Environmental data were taken throughout the experimental period and means were recorded (*Figure 4.3.1* and *Figure* 4.3.2). Soil physical and chemical characteristics (*Table 4.3.1*) were taken prior establishment of the experiments.

4.3.1.3 Experimental design, layout and measurements

Experimental design, layout and common measurements like growth data, relative water content and leaf chlorophyll all are described under Chapter 3.

4.3.1.4 Cultural practices

The experiments were conducted from August – November 2017. Fertilizer was applied at the rate of 20 kg (N), 60 kg (P_2O_5) and 40 kg (K_2O) per hectare. Sources of nutrients N, P and K were Urea (46% N), triple super phosphate [46 % phosphorus pentoxide (P_2O_5)] and muriate of potash [60 % potassium oxide (K_2O)] respectively. P_2O_5 and K_2O fertilizers were applied and incorporated in to the soil at sowing while N was applied one week after emergence. Neither

fungicide nor insecticide was applied, as there was no insect infestation or disease outbreak observed during the trial. Weeding and water application are as described in Chapter 3.

4.3.1.5 Data collection and analysis

Soil moisture data

Soil moisture in the field was measured by PR2 soil profile probe (Delta T Devices, UK, 1971) for compensation of moisture loss while maintaining the moisture needed. Three access tubes per replication (making 9 access tubes per site) were inserted into the soil for the whole duration of the experiment. Each tube was intended to monitor the soil content per water regime, main plots (control, water deficit stress during flowering and water deficit stress during flowering). More details on plot size and experiment layout are available in chapter 3 under section 3.6.1.

4.3.2 Results

4.3.2.1 Environmental data

The environmental data recorded were; maximum day temperatures, minimum day temperatures, maximum night temperatures, minimum night temperatures and relative humidity (*Figure 4.3.1* and *Figure 4.3.2*). Other environmental parameters include; pan evaporation and sunshine hours (*Figure 4.3.2*).

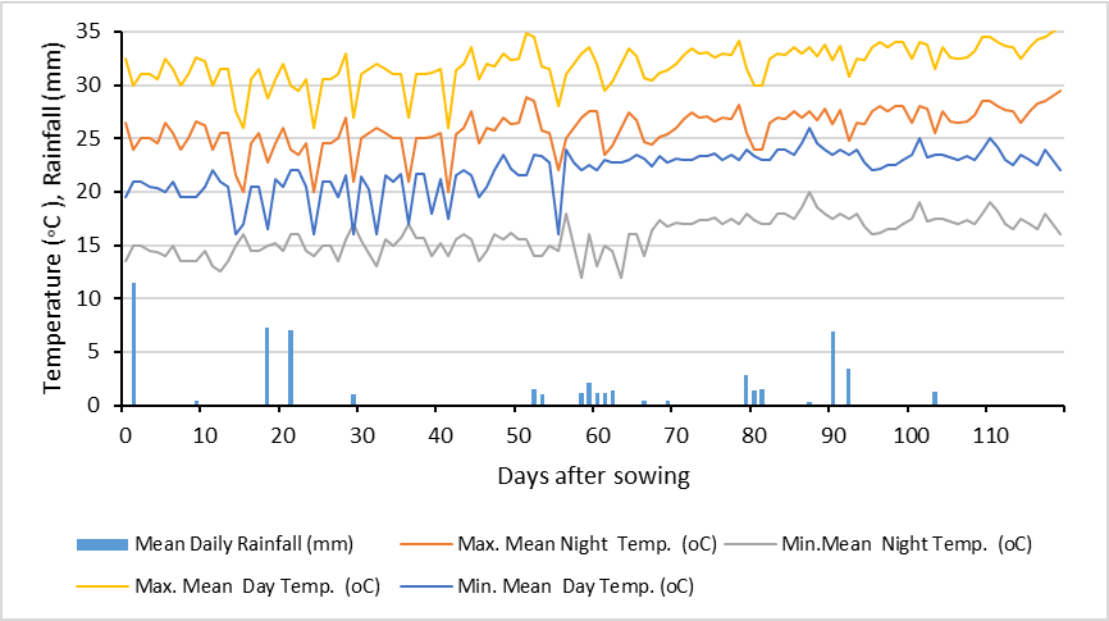


Figure 4.3.1: Environmental weather conditions (Day and night temperature and rainfall) during the experiment conducted at Naliendele Agricultural Research Institute Mtwara Tanzania between August and December 2017.

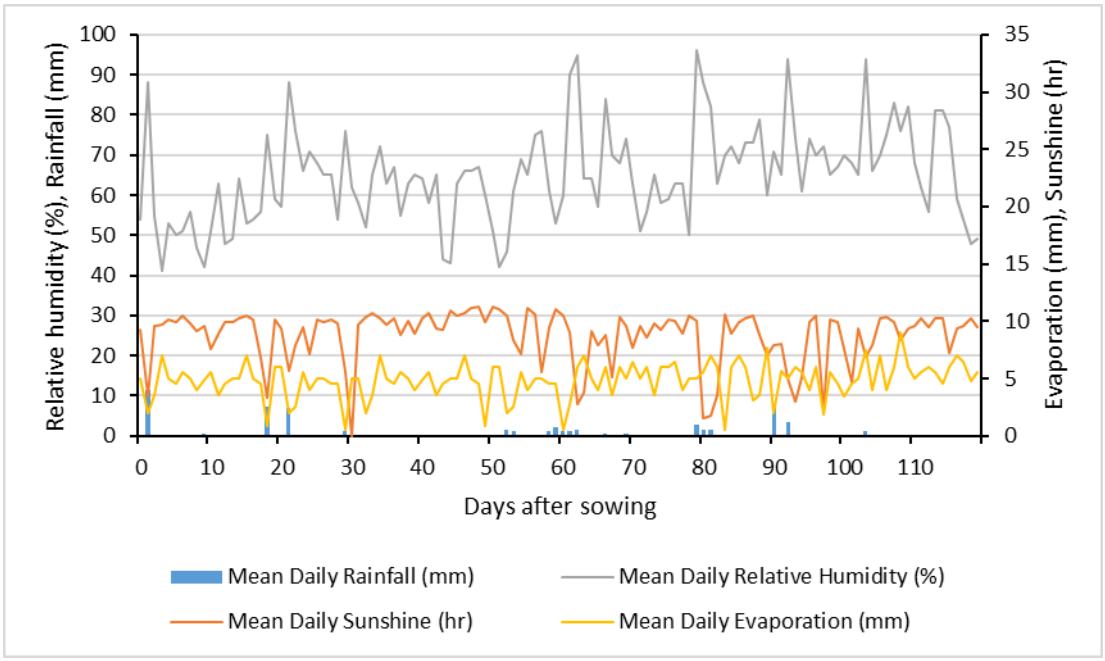


Figure 4.3.2: Environmental weather conditions (Relative humidity, mean daily sunshine, rainfall and mean daily evaporation) during the experiment conducted at Naliendele Agricultural Research Institute Mtwara Tanzania between August and December 2017.

4.3.2.2 Soil characteristics of the study area

Soil physical and chemical properties of the both Mizambaraoni (site 1) and Mpakani (site 2) are presented in (*Table 4.3.1*). Soil characterization was done before start of the experiments.

Table 4.3.1: Soil physical and chemical properties of the experimental sites

		Mizambaraoni	Mpakani
Soil Ph (1:2.5)	(in H_20)	5.02	5.06
	(in 0.01M $CaCl_2$)	4.86	4.94
Particle Size Analysis (Boyocous hygrometer method)	% Clay	12.20	13.60
	% Silt	3.28	2.86
	% Sand	84.52	83.54
	Textural class	Loamy sand	Loamy sand
Total Nitrogen (%) (Kjeldahl Method)		0.05	0.04
Organic Carbon (%)		0.44	0.47
Available Phosphorous (mg/kg) (Bray-P1 Method)		1.95	1.97
Cation Exchange Capacity (Cmol/kg)		7.33	7.43
Exchangeable Bases (cmol/kg)	Ca2+	1.06	1.08
	Mg2+	0.39	0.41
	K+	0.15	0.18
	Na+	0.09	0.08

4.3.2.3 Soil moisture content

The moisture content distribution for the sites 1 and 2 are shown in *Figure 4.3.3.* The soil moisture content distribution follows the same trend in both sites. Results reveal that soil moisture content decreased with water deficit stress. Drought significantly ($p < 0.001$) reduced soil moisture content during both water deficit stress stages at Mizambaraoni and Mpakani sites. Control plots were found to maintain soil moisture content closer or equal to field capacity (*Figure 4.3.3*). Plots that were water deficit stressed during pod development had relatively lower soil moisture storage than water deficit stressed plants during flowering. However, the moisture content distribution was sequential with highest in the deepest horizon (100 cm) and lowest in the uppermost layer (30 cm) (*Figure 4.3.3*).

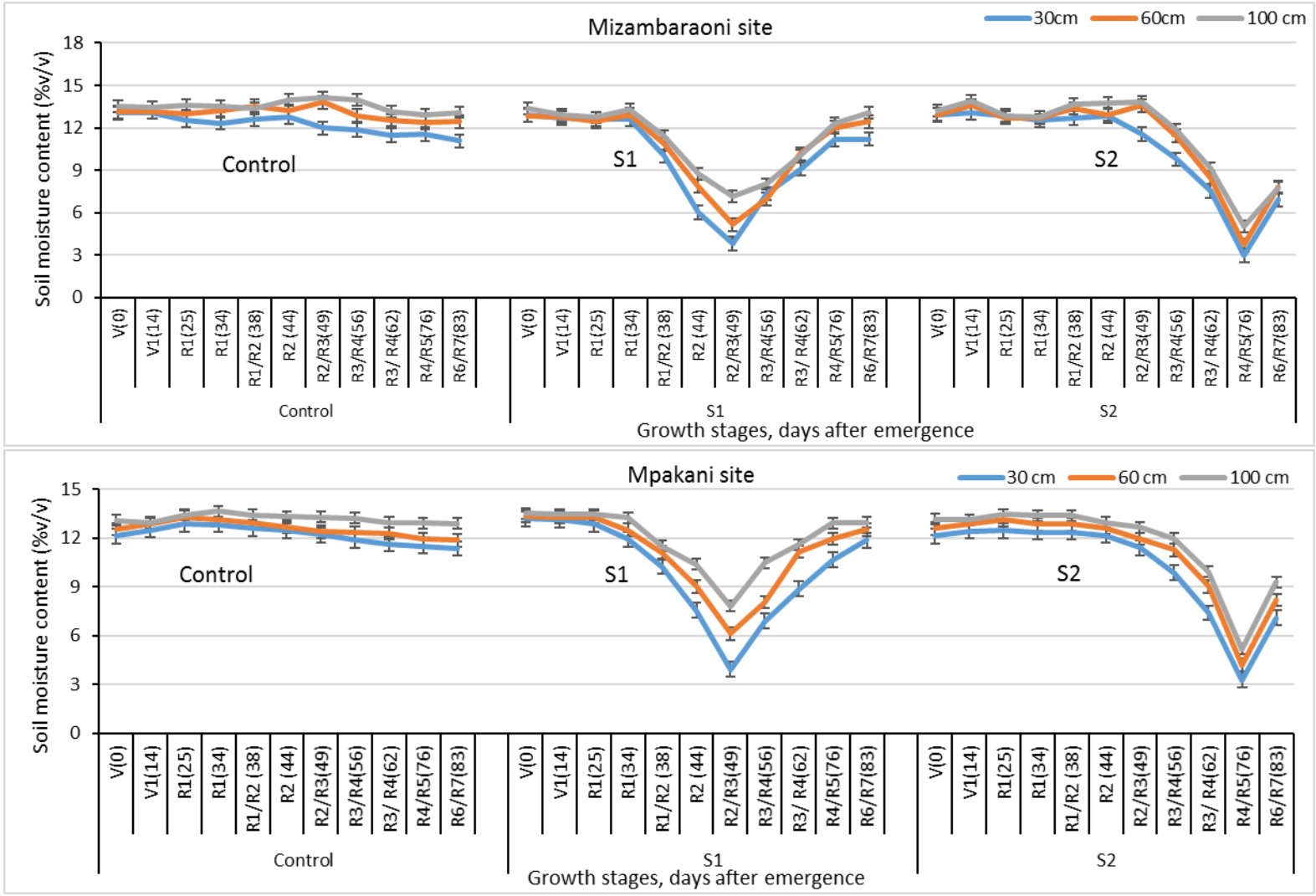


Figure 4.3.3: Effect of water deficit on soil moisture content under different depths at Mizambaraoni and Mpakani during the experiment conducted at Naliendele Agricultural Research Institute Mtwara Tanzania between August and December 2017. Control = well-watered throughout the trial, S1 = water deficit stress during flowering, S2 = water deficit stress during pod development. R1 = Flowering, R2 = Beginning peg, R3 =Beginning pod, R4 = Full pod, R5 = Beginning seed, R6 = Full seed. (n = 6).

4.3.2.4 Above ground crop traits

Phenological stages

Data for phenological stages are shown in *Figure 4.3.4* for both Mizambaraoni (site 1) and Mpakani (site 2) sites. Some of phenological stages (flowering and maturity) were significantly ($p < 0.05$) affected by water deficit stress. Bambara groundnut landraces differed significantly ($p < 0.001$) in all growth stages. The interaction between bambara groundnut landraces and water regimes were not significant ($p > 0.05$) for all phenological stages. In both sites, there was no significant differences ($p > 0.05$) on days to emergence among water regimes or landraces. The effect of soil water deficit stress was significant ($p < 0.05$) on days to flowering, days to podding and days to maturity at Mizambaraoni site, while in Mpakani site there was no significant differences ($p > 0.05$) among the water regimes *(Figure 4.3.4*). With the exemption of days to emergence, landraces differed significantly ($p < 0.001$) in all phenological stages in both sites (*Figure 4.3.4*). Among bambara groundnut landraces, S19-3 showed the least days to all of the growth stages, followed by DodR. MNANJE the groundnut had the least days to flowering, 50% flowering, podding and maturity.

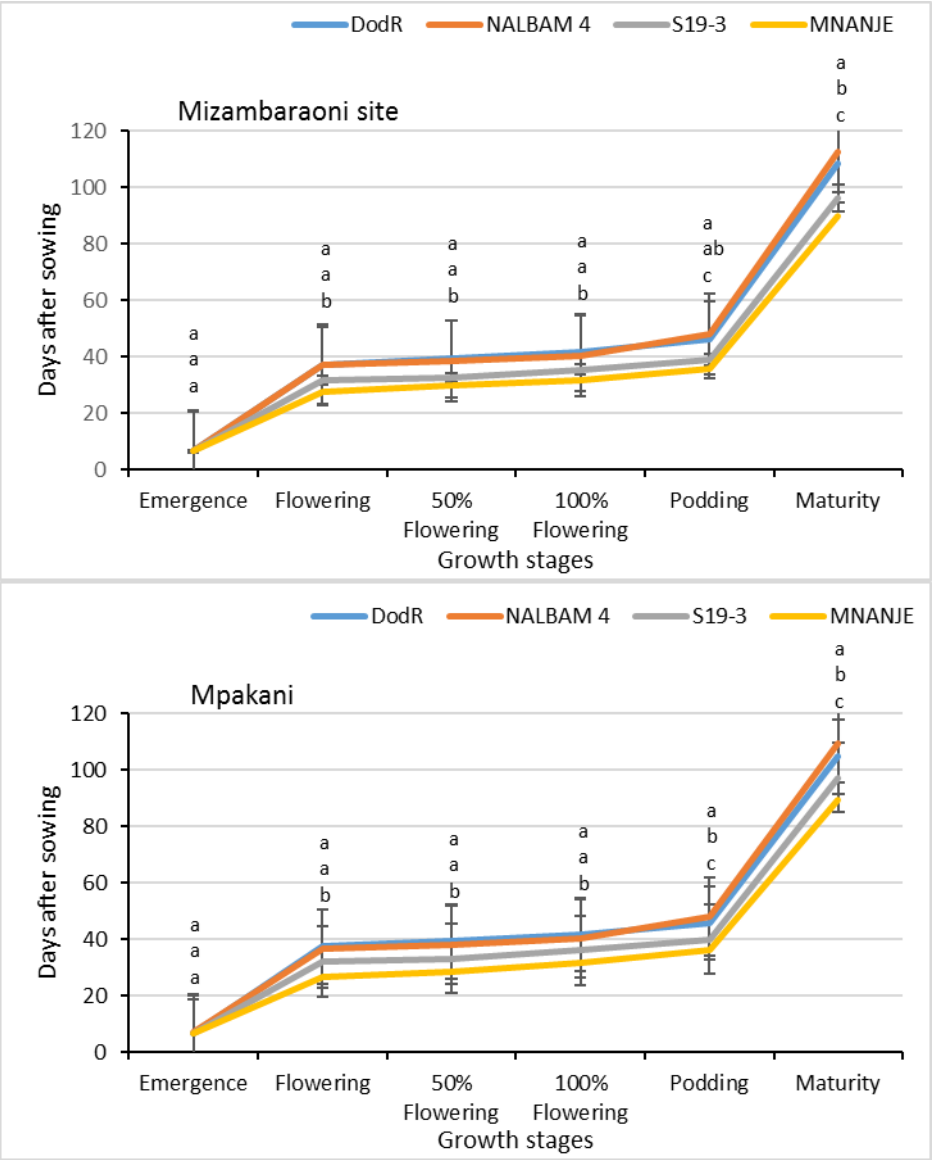


Figure 4.3.4: Variations in number of days to different growth stages of bambara groundnut and groundnut landraces under field conditions at Naliendele Agricultural Research Institute, Tanzania during 2017 dry cropping season. (n = 3).

Leaf chlorophyll content (CCI)

Lack of enough water supply had detrimental effects ($p < 0.05$) on chlorophyll content index in bambara groundnut landraces in both Mizambaraoni (site 1) and Mpakani (site 2) sites (*Figure 4.3.5*). Whereas, limited supply of soil water significantly ($p < 0.05$) improved chlorophyll content in groundnut (MNANJE) in both sites (*Figure 4.3.5*). The interaction among landraces and water treatments over time was not significant ($p > 0.05$). With respect to bambara groundnut landraces, S19-3 showed the highest chlorophyll content index and the

lowest was observed in DodR. In all landraces, plants that were water deficit stressed during flowering were more affected as compared to plants that were water deficit stressed during pod development (*Figure 4.3.5*). MNANJE accumulated the highest chlorophyll content as compared to bambara groundnut landraces (*Figure 4.3.5*). Higher values of chlorophyll content in MNANJE was found in water deficit stressed plants while for all bambara groundnut landraces, higher values of CCI was found in well-watered plants (*Figure 4.3.5*). Regardless of water regime, chlorophyll content index increased with plant growth and started to decline as plants got older (*Figure 4.3.5*).

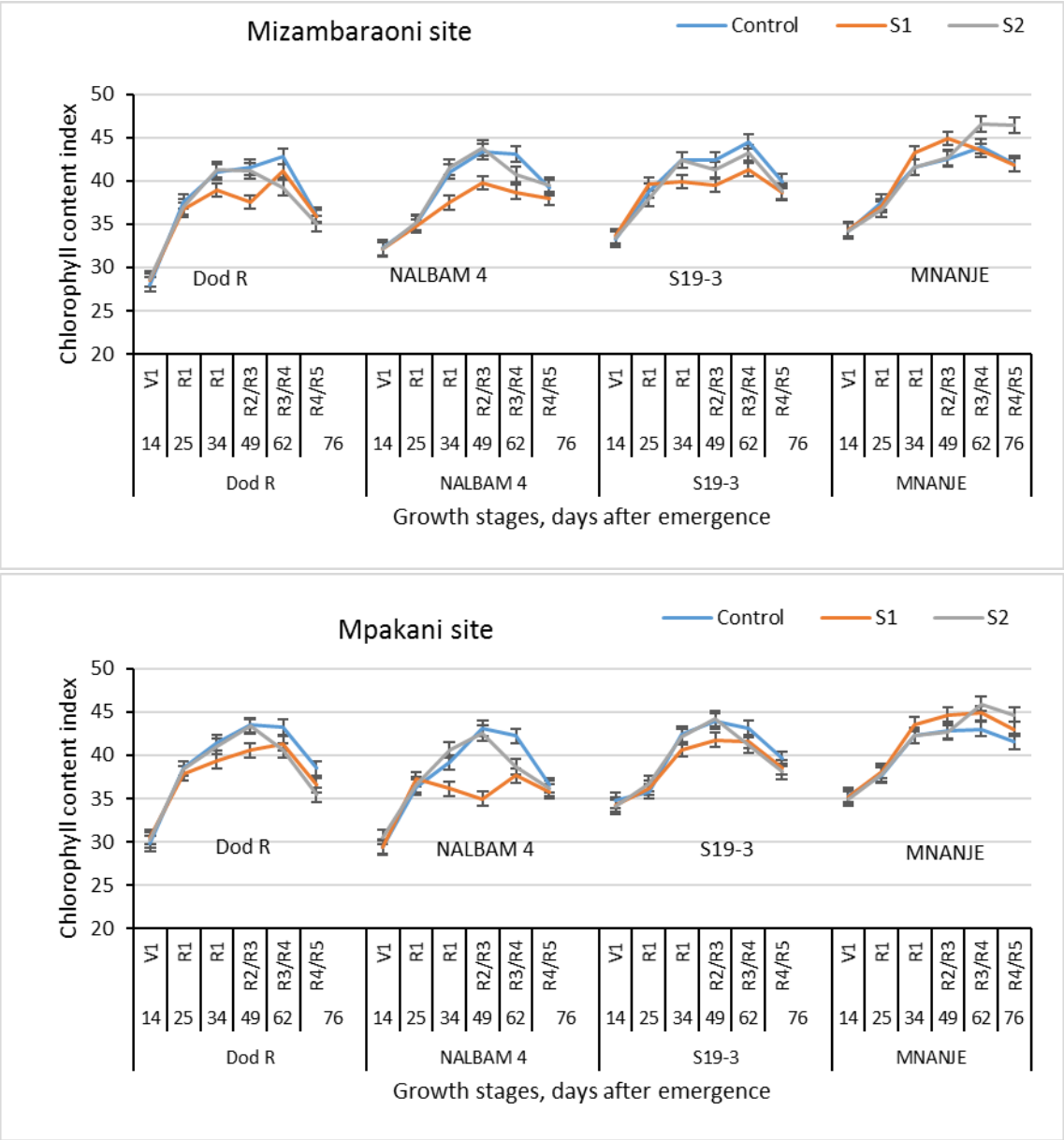


Figure 4.3.5: Effect of water deficit stress on chlorophyll content index in field experiments conducted at Mizambaraoni and Mpakani sites at Naliendele Agricultural Research Institute Mtwara, Tanzania in 2017 dry season. (n = 18).

Stomatal conductance

A consistent pattern was observed for results of stomatal conductance (gs) in both sites. Water scarcity significantly ($p < 0.001$) decreased stomatal conductance in both bambara groundnut and groundnut. Bambara groundnut landraces and the interaction between bambara groundnut landraces and water regimes all showed significant differences ($p < 0.001$) in both sites (*Table 4.3.2*). Higher percentage decrease in stomatal conductance was

found during flowering stage as compared to pod development stage in both sites. Among bambara groundnut landraces, DodR gave the highest stomatal conductance values in well-watered plants (*Table 4.3.2*). In contrast, in water limited conditions, S19-3 recorded higher values than the other bambara groundnut landraces (*Table 4.3.2*). The least percentage changes in gs among bambara groundnut landraces in both stress periods and sites were found in S19-3, while the highest changes were found in DodR. In both cases, water regimes and sites, MNANJE showed superiority over bambara groundnut landraces. With the exception of percentage decrease in gs shown during pod development in Mpakani site, MNANJE revealed highest stomatal conductance values and the least percent decrease in gs between control and stressed plants at Mizambaraoni and Mpakani sites (*Table 4.3.2*). At Mpakani site, the least percentage change was found in S19-3 and the highest change in DodR. Generally, Mpakani site showed higher values of stomatal conductance relative to Mizambazaoni (*Table 4.3.2*).

Relative leaf water content (RWC %)

Significant variations ($p < 0.001$) existed among the drought treatments and control plots in both sites *(Table 4.3.2*). Bambara groundnut landraces revealed significant ($p < 0.001$) differences in both sites. Interaction between water treatments and landraces also revealed significant ($p < 0.001$) changes in both sites. The reduction in RWC was more pronounced during flowering than during pod development. Among bambara groundnut landraces, S19-3 was superior both in values of RWC and lowest percentage decrease. There was no consistency on RWC values and percentage change between DodR and NALBAM 4 (*Table 4.3.2*). MNANJE, the groundnut, had the highest RWC values and least percentage decrease in all water regimes and both sites as compared to bambara groundnut landraces.

Table 4.3.2: Water deficit stress on relative water content and stomatal conductance at Mizambaraoni (Site 1) and Mpakani (Site 2) during the experiment conducted at Naliendele Agricultural Research Institute Mtwara, Tanzania between August and December 2017 dry season.

Treatments		Stomatal conductance (mmol m^{-2} s^{-1})								Relative water content (%)							
		Mizambaraoni				Mpakani				Mizambaraoni				Mpakani			
		S1	%Δ	S2	%Δ	S1	%Δ	S2	%Δ	S1	%Δ	S2	%Δ	S1	%Δ	S2	%Δ
Water regimes	Control	335.70^{a}		282.00^{a}		360.5^{a}		293.61^{a}		89.64^{a}		89.45^{a}		91.60^{a}		90.56^{a}	
	Stressed	97.60^{b}	-71	88.50^{c}	-69	98.10^{c}	-73	121.34^{c}	-59	64.00^{b}	-29	64.56^{b}	-28	67.63^{b}	-26	63.75^{c}	-30
Landraces	Dod R	265.80^{a}		201.90^{a}		287.82^{a}		221.22^{a}		80.07^{b}		78.70^{c}		85.44^{a}		78.08^{b}	
	NALBAM 4	237.90^{b}		179.40^{b}		175.93^{c}		210.50^{b}		80.52^{b}		80.47^{b}		79.96^{b}		79.47^{b}	
	S19-3	263.10^{a}		201.50^{a}		269.1^{b}		221.73^{a}		82.87^{a}		83.02^{a}		84.98^{a}		83.35^{a}	
	MNANJE	255.56		194.28		311.4		290.8		86.97		85.48		86.55		86.11	
Interaction																	
Dod R	Control	353.80^{ab}		301.10^{a}		390.00^{a}		315.70^{a}		89.07^{a}		88.60^{a}		91.18^{a}		90.85^{a}	
	Stressed	88.00^{g}	-75	75.80^{f}	-75	86.90^{d}	-78	82.51^{d}	-74	62.73^{c}	-30	60.03^{d}	-32	73.84^{b}	-19	62.14^{d}	-32
NALBAM 4	Control	317.10^{de}		274.60^{b}		344.20^{b}		267.92^{b}		89.45^{a}		89.98^{a}		90.45^{a}		89.65^{a}	
	Stressed	86.10^{g}	-73	79.80^{f}	-71	93.71^{d}	-73	82.90^{c}	-69	61.66^{c}	-31	64.00^{c}	-29	59.66^{d}	-34	60.67^{d}	-32
S19-3	Control	336.10^{ac}		270.30^{b}		347.32^{b}		297.12^{a}		90.40^{a}		89.76^{a}		93.18^{a}		91.2^{a}	
	Stressed	118.80f	-65	110.10^{e}	-59	113.61^{c}	-67	101.60^{d}	-66	67.61^{b}	-25	69.66^{b}	-22	69.38^{c}	-26	68.44^{c}	-25
Water regimes	p-value	<.001		<.001		<.001		<.001		<.001		<.001		<.001		<.001	
Landraces	p-value	<.001		<.001		<.001		0.006		<.001		<.001		<.001		<.001	
Interaction	p-value	<.001		<.001		<.001		<.001		0.005		<.001		<.001		<.001	
MNANJE	Control	392.60^{a}		393.80^{a}		399.40^{a}		378.01^{a}		94.41^{a}		91.84^{a}		91.08^{a}		92.75^{a}	
	Stressed	213.70^{b}	-46	269.30^{c}	-32	133.71^{b}	-67	123.8^{b}	-67	72.14^{b}	-24	74.44^{c}	-19	74.15^{b}	-18	74.78^{b}	-19
	p-value	<.001		<.001		<.001		<.001		<.001		<.001		<.001		<.001	

Means within the same column followed by the same letter are not significantly different at 5% level based on Duncan's Multiple Range Test. % Δ = Percentage change between control and water stressed plants, S1 = water deficit stress during flowering, S2 = water deficit stress during pod development. (n = 6).

4.3.2.5 Rooting depth

The results of rooting depth for Mizambaraoni and Mpakani sites are shown in *Table 4.3.3*. Similar trend of variations existed in both sites with respect to water regimes and landraces. Insufficient water supply substantially ($p < 0.001$) decreased rooting depth compared to control. Rooting depth varied significantly ($p < 0.001$) among the bambara groundnut landraces. Interaction among water treatments and bambara groundnut landraces varied significantly ($p < 0.001$) at Mizambaraoni during flowering, while at Mpakani was significant ($p < 0.05$) during pod development (*Table 4.3.3*). In both sites, higher percentage changes were observed in plants that were water deficit stressed during flowering than plants that were water deficit stressed during pod development.

Among bambara groundnut landraces, rooting depth in all water regimes and both sites followed the trend; S19-3 > DodR > NALBAM 4 (*Table 4.3.3*). There was no consistent trend in percentage decrease in rooting depth. S19-3 showed the highest percent decrease (27%) during flowering and least percent decrease (12%) during pod development at Mizambaraoni site. At Mpakani site S19-3 gave the least percent decrease during both flowering (19%) and pod development (5%) water stress periods. Although analysis was done separately between the two species, it is obvious that, MNANJE outweighed all the bambara groundnut landraces in both sites and all water regimes (*Table 4.3.3*) in rooting depth. In addition, MNANJE the groundnut, revealed the least percentage changes in all water regimes and sites. In both species, well-watered plants revealed higher rooting depths compared to water deficit stressed plants during both water deficit stress periods and in both sites.

Table 4.3.3: Effect of soil water deficit stress on bambara groundnut and groundnut rooting depth in field experiments conducted at two sites in 2017 dry season at Naliendele Agricultural Research Institute Mtwara, Tanzania

		Rooting depth (cm)							
		Mizambaraoni				Mpakani			
		S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ
Water regimes	Control	27.24[a]		38.39[a]		29.83[a]		39.87[a]	
	Stressed	20.40[b]	-25	33.06[b]	-14	23.51[c]	-21	35.10[b]	-12
Landraces	DodR	24.94[b]		33.16[b]		26.28[b]		36.47[b]	
	NALBAM 4	19.92[c]		30.87[c]		24.89[c]		31.97[c]	
	S19-3	30.36[a]		39.34[a]		32.20[a]		41.57[a]	
	MNANJE	32.23		40.92		31.26		43.47	
Interaction									
DodR	Control	27.37[b]		37.27[b]		28.77[c]		40.20[a]	
	Stressed	19.43[d]	-29	32.43[cd]	-13	21.40[fg]	-26	34.43[b]	-14
NALBAM 4	Control	21.10[cd]		34.63[bc]		26.57[ef]		36.13[b]	
	Stressed	17.53[d]	-17	28.80[e]	-17	21.43[g]	-19	29.93[c]	-17
S19-3	Control	33.27[a]		43.27[a]		34.17[a]		43.27[a]	
	Stressed	24.23[bc]	-27	37.93b	-12	27.70b[c]	-19	40.93[a]	-5
Water regimes	p-value	0.001		<.001		<.001		<.001	
Landraces	p-value	<.001		<.001		<.001		<.001	
Interaction	p-value	<.001		0.26		0.23		0.03	
MNANJE	Control	36.27[a]		43.70[a]		37.17[a]		45.47[a]	
	Stressed	30.40[b]	-16	41.83[b]	-4	31.30[c]	-16	43.27[b]	-5
	p-value	<.001		0.002		0.001		0.002	

Means within the same column followed by the same letter are not significantly different at 5% level based on Duncan's Multiple Range Test. % Δ = Percentage change between control and water stressed plants, S1 = water deficit stress during flowering, S2 = water deficit stress during pod development. (n = 6).

4.3.3 Discussion

Soil moisture

Available soil water during the cropping season was measured under well-watered plots and water limited plots (during flowering and pod development). The soil moisture distribution trend and variation were similar at both Mizambaraoni and Mpakani sites. Soil moisture content was monitored at 30, 60 and 100 cm depths (*Figure 4.3.3*). The highest soil water content values were observed under control plots at 100 cm depth, while the lowest values were found in plots that were water deficit stressed during flowering at the 30 cm soil depth. Regardless of the water regime and soil depth, the current study revealed a decrease in soil

moisture with plant growth. Similarly, decrease in soil moisture content with plant growth has been informed in groundnut (Painawadee et al., 2009; Puangbut et al., 2009; Sukanya and Mahendran, 2018) and in bambara groundnut (Jorgensen et al., 2011; Al Shareef et al., 2014). In the current study, higher percentage reductions were observed during flowering water deficit stress (*Figure 4.3.3*). These findings are in agreement with findings by Jaimez et al. (2000) in bonnet pepper (*Capsicum chinense* Jacq) who reported higher water use during flowering. Study by Karim et al. (2018) in cowpea revealed that, insufficient water supply was more severe during flowering stage. The higher demand of water observed in the present study can be explained by the fact that, during flowering stage plants had the highest number of active leaves and hence higher rates of transpiration. In addition, during flowering, plants demand more resources such as water (Vurayai et al., 2011a) to drive reproductive development processes. The current study suggests that, flowering stage is the critical stage at which enough water supply must not be underestimated.

Phenological stages

In the current study, insufficient water supply did not show any effects on phenology of the tested crop materials (bambara groundnut and groundnut) in both sites (Mizambaraoni and Mpakani) (*Figure 4.3.4*). However, significant differences existed among bambara groundnut landraces in both sites. The current results agree with findings by Arunachalam and Kannan, (2013) in groundnut but contradict the findings by Madukwe et al. (2011) who found delayed flowering in bambara groundnut due to insufficient water supply. The contradictions observed here might be due to the fact that, the water deficit stress in the current study was imposed just after the start of flowering; until this point all plots were equally supplied with water.

Regardless of water regime, S19-3 was found to flower and mature earlier in both sites compared to other bambara groundnut landraces (DodR and NALBAM 4). Mabhaudhi and Modi (2013) reported existence of variations among both water regimes and bambara groundnut landraces in days to flowering and maturity. Other results by Madukwe et al. (2011) showed that, water deficit significantly increased days to flowering but not to 50% maturity in bambara groundnut. The differences observed among bambara groundnut landraces implies that, attainment of different phenological stages is also attributed by genotypic differences, which exist among the landraces in the current study. Hall and Patel (1985) reported that early maturing cowpea varieties have proved more useful in some dry environments and years because of their ability to escape drought.

MNANJE the groundnut, showed least days to reach all of the growth stages compared to bambara groundnut landraces. MNANJE flowered and matured far earlier as compared to bambara groundnut landraces (*Figure 4.3.4*). Blum (2005) related early flowering with reduced plant growth and was an important strategy in mitigation of water loss due to drought. Early flowering is categorized as a mechanism for drought escape (Araus et al., 2002). In this context, MNANJE and S19-3 are more advantaged with respect to performance under drought conditions as compared to DodR and NALBAM 4 (*Figure 4.3.4*). Though MNANJE matured much earlier (83 DAE) than S19-3 (91 DAE), the current findings suggests that the two are capable of completing their life cycles in a short period before terminal drought. Hence, they use a drought escape mechanism to survive in dry environments. Both MNANJE and S19 -3 are valuable resources in breeding programmes targeting early maturing traits as one of the strategies of improving yield under drought conditions.

Chlorophyll Content

Chlorophyll content index increased with plant age at early growth stages but decreased at late stages of growth in both bambara groundnut and groundnut in both sites. The current findings are in line with findings by Rodrigues (2004); Mauromicale et al. (2006). Water deficit stress is also known to reduce chlorophyll content in some crops while increasing in others. Drought stress has been found to reduce chlorophyll content index in bambara groundnut (Mabhaudhi and Modi, 2013; Meena and Massawe, 2013) and maize (Anjum et al., 2011). Vurayai et al. (2011a), found no significant changes in chlorophyll content index between water deficit stressed and well-watered bambara groundnut plants. Nonetheless, water deficit stress has been found to increase chlorophyll content in groundnut (Arunanyark et al., 2009; Chakraborty et al., 2015; Mamadou et al., 2016) and in sesame (*Sesamum indicum* L.) (Mensah et al., 2006).

The current results, which indicated reduced chlorophyll content index in bambara groundnut and increased groundnut under water stress conditions agree with previous reports. The increase in chlorophyll content index shown in this experiment might have been attributed to thicker leaves (reduced leaf area) of stressed groundnut plants (Nageswara Rao and Wright, 1994). Arunyanark et al. *(*2008) described the ability of groundnut in maintaining chlorophyll production in water limited environments as a worthy indicator in assessing the strength of groundnut to survive under water scarce conditions. The higher production of chlorophyll content shown by MNANJE under insufficient water supply (*Figure 4.3.5*) implies that MNANJE can carry on photosynthesis under drought conditions. The decreased chlorophyll content index in bambara groundnut landraces can be illustrated by increased disruption of chlorophyll pigments caused by metabolic imbalance (Sikuku et al., 2012).

Limited supply of water is said to promote building up of reactive oxygen species (ROS) which affects metabolic tissues and hence chlorophyll content (Sikuku et al., 2010b). Although bambara groundnut landraces reduced CCI under water stress, S19-3 was found to maintain relatively high chlorophyll content as compared to DodR and NALBAM 4 (*Figure 4.3.5*). Maintaining relatively higher values of chlorophyll content may be associated with a relative increase in photosynthetic activities and ultimately crop yield. Chlorophyll stability during drought might be a promising criterion for selection for drought resistance in both bambara groundnut and groundnut.

Stomatal conductance

In the current investigation, the stomatal leaf conductance declined following imposition of water deficit stress, which agrees with previous findings in bambara groundnut (Collinson et al., 1997; Cornellisen, 2005; Vurayai et al., 2011b; Chai et al., 2016), in chickpea (Mafakheri et al., 2010) and in groundnut (Lauriano et al., 2004; Songsri et al., 2013; Junjittakarn et al., 2016). Additionally, the results agree with the study by Nageswara Rao et al. (1988) and Jongrungklang et al. (2013), who testified that water deficit could considerably decrease transpiration.

Closing stomata is a first response of plant against decreasing availability of soil moisture and it is considered as a drought avoidance strategy (Farooq et al., 2009). Stomatal closure is also a characteristic of increased water use efficiency under drought stress but with reduction in final yield (Blum, 2009). With respect to this investigation, DodR and Nalbam4 showed low transpirational water use in water limited environments. By showing low transpirational water use, plants may be reserving leaf water at the expense of photosynthesis and reduced biomass as well as yield. Both MNANJE and S19-3, although from different species, maintained

higher transpirational water use thus touted to increase photosynthesis and final economic yield. Maintaining flow of CO_2 and water vapour (stomatal conductance), and so photosynthesis, influenced drought resistance in water limited plants (Jongrungklang et al., 2012). In this study, MNANJE and S19-3 showed a lower reduction in stomatal conductance compared to DodR and NALBAM 4 (*Table 4.3.2*). Both MNANJE and S19-3 maintained high values of stomatal conductance in both sites under drought stress, indicating high water transpiration, increased photosynthesis and subsequently yield.

Relative leaf water content (RWC %)

Water is very important to plant metabolism as it plays a vital role in cell division and expansion. The RWC of plant leaves is under control of stomata; closing of stomata is reported as the earliest responses to limited water supply (Cechin et al., 2015). Under insufficient water supply, most of plants are adversely affected. In the current study, reduction in RWC due water deficit stress significantly differed among the bambara groundnut landraces. Various studies have reported similar results in bambara groundnut (Collinson et al., 1997; Vurayai et al., 2011a; Muhammad et al., 2015), in groundnut (Nautiyal et al., 2002; Chakraborty et al., 2013; Madhusudhan and Sudhakar, 2014b), in pigeonpea (Kumar et al., 2011) and in sunflower (Cechin et al., 2015).

The differences observed in the current study might have been caused by the genetic background of the landraces. Bambara groundnut landrace S19-3 consistently maintained high values of relative water content compared to DodR and NALBAM 4 in both sites (*Table 4.3.2*). Maintaining high RWC under water stress conditions might be one indicator for drought resistance (Nautiyal et al., 2002). Although maintaining water under water deficit stress is partly associated with reduction in net photosynthesis, it may also be contributed to

by accumulation of proline as it acts as osmoregulator in plant leaves (Collinson et al., 1997). Care must be taken when considering traits to improve for drought resistance. It must be noted that, maintenance of a relative leaf water content during stress is an important defensive mechanism; and this may be achieved by minimizing water loss and maximizing water uptake (Barnabás et al., 2008). Maintenance of relative water content under insufficient water supply is associated to mechanisms to sustain turgor (Chai et al., 2016). In the current research, the high relative water content values shown by MNANJE and S19-3 under water deficit stress (*Table 4.3.2*) suggest that plants have the capacity to maximize water uptake and maintain turgor rather than to minimize water loss. In subsequent studies carried our as part of the present study (see chapters 4 – 6), MNANJE and S19-3 were found to have deeper roots for maximization of water uptake and high accumulation of proline for turgor maintenance against drought.

Rooting depth

Limited water supply significantly ($p < 0.001$) decreased rooting depths in both sites (*Table 4.3.3*). The present results agree with findings by Boontang et al. (2010), Girdthai et al. (2010), Junjittakarn et al. (2014) in groundnut and Belachew et al. (2018) in faba bean. Regardless of water regimes, bambara groundnut landraces significantly ($p < 0.001$) varied in rooting depths. This implies that, water stress is not the only factor contributing to the differences on rooting depths. The other factor could also be inherited root characteristics within the bambara groundnut landraces. Other authors (Harris et al., 1988; Junjittakarn et al., 2014) have reported existence of differences in rooting depth among groundnut genotypes. The current results revealed that, bambara groundnut landrace S19-3 showed relatively deeper roots while NALBAM 4 was found to produce shallow rooting depths across all water regimes and sites (*Table 4.3.3*). This suggests that, among bambara groundnut landraces, S19-3 is more

favoured to soil moisture available in deeper horizons and hence can mitigate drought through avoidance and or resistance mechanisms. However, MNANJE the groundnut, showed superiority on rooting depths across the water regimes and sites. This suggests that, MNANJE can perform better in dry conditions as compared to bambara groundnut landraces used in the current study. Since water is more abundant in deeper horizons in dry environments, plants with deeper roots have a growth advantage in water limited conditions (Sponchiado et al., 1989; Ho et al., 2005). Deeper roots can extract more soil water stored in deeper soil profile thus avoiding water deficits at critical growth stages. Pirnajmedin et al. (2015) explained the development of expanded or deep root systems as one of factors associated with drought resistance mechanisms. Rooting depth therefore, can predict the drought resistance of bambara groundnut and groundnut.

Deep-rooted landraces like MNANJE and S19-3 have advantage over shallow rooted ones. By combining the pre-existing potential and the deeper root system observed in MNANJE and S19-3; the two can be utilized in crop diversification and intensification under drought environments. Subsequently improvement of livelihoods for smallholder farmers.

4.3.4 Key observations and findings

The results from the two experiments followed similar trends for both water regimes and plant materials used. Furthermore, all physiological parameters studied showed similar patterns in both sites. Water deficit stress decreased stomatal conductance, relative water content and rooting depth in both bambara groundnut and groundnut. Chlorophyll content index was decreased in all bambara landraces but increased in groundnut. Among the bambara groundnut landraces S19-3 was the best landrace under insufficient water supply because it maintained high RWC, chlorophyll content index, stomatal conductance and

deeper roots. Differences among bambara groundnut landraces were mainly found in water related parameters, which indicates adaptations in stomata regulation. MNANJE the groundnut overweighed all bambara groundnut landraces in all aspects. S19-3 and MNANJE might be identified as useful candidates for cultivation in dry areas. RWC, stomatal conductance, chlorophyll content will be important for selecting traits for drought resistance genotypes.

Results from the three field experiments showed that, bambara groundnut landraces were negatively affected by water deficit stress and low temperatures experienced during the cropping season. During the first field experiment in 2016, landrace NALBAM 2 was the most affected by the low temperatures compared to NALBAM 4, which led to drying and eventual death of the majority of plants. Similarly, in the successive field experiments in 2017, bambara groundnut landraces were affected by low temperatures. However, landrace S19-3 was found to be the least affected (visual observation and no data available) and probably may contain genes to withstand low temperatures (Al Shareef et al., 2014; Bonthala et al., 2016). On the other hand, MNANJE, the groundnut was not affected by low temperatures in all three experiments.

4.3.5 Challenges observed under the current field experiments

Conducting field experiments is vital for the selection of crops and development of improved varieties, which are suitable for the changing climate. However, water deficit stress experiments in real field conditions can be successful in pre identified and selected areas. In both field experiments, 1 (2016 dry season), 2 and 3 (2017 dry season), bambara groundnut landraces were adversely affected by the weather in both years and sites. Pod yields were only obtained from MNANJE, the groundnut. There was negligible harvest from bambara

groundnut landraces. The experiments were conducted during dry seasons, (dry, cool and windy conditions experienced during the months of August to December 2016 and 2017). Bambara groundnut landraces were affected by the prevailing weather conditions (e.g. low temperatures) (*Figure 4.2.1*), since bambara groundnut is known to be a warm temperature crop. Usually the optimum temperature (T_o) for bambara groundnut ranges from 28.5 to 32.5°C (Linnemann and Azam-Ali, 1993; Swanevelder, 1998); 20–28°C (Atkinson et al.,2013; Ibraheem et al., 2014). Low temperatures, less than 16 ^oC (*Figure 4.2.1*), experienced during the experiments might have resulted to chilling effect that affected leaves and then the entire plants of some of bambara groundnut landraces (Raison and Lyons, 1986; Bloom et al., 2004; Chinnusamyetal, 2007). Chilling of susceptible plants affects all water treatments and led to water loss from the plants, followed by permanent wilting (Vernieri et al., 1991; Boese et al., 1997; Bloom et al., 2004). This may have been the case for bambara groundnut plants during the course of all the current field experiments. Zondi (2012) found that bambara groundnut landraces were affected by low temperatures. In different experiments on bambara groundnut conducted during summer and winter, the yield obtained during summer were far higher than those obtained during winter (Sinefu, 2011; Zondi, 2012). The study by Zondi (2012) on bambara groundnut revealed that, plants grown at 21/15°C (day/night) had stunted growth and failed to produce seed yields.

Further studies are encouraged to further investigate the effect of low temperatures on growth and development of bambara groundnut. Such studies should include a large number of bambara groundnut landraces/genotypes to screen for adaptation to low temperatures.

4.3.6 Conclusion

In all three experiments conducted under field conditions, both species showed resilience to drought. Results from the current research revealed MNANJE and S19 – 3 as drought resistant compared to DodR and NALBAM 4. It was also found that, more than one drought adaptation mechanisms were utilized by both bambara groundnut and groundnut. Drought avoidance and escape mechanisms were experienced in S19-3 and MNANJE, while DodR and NALBAM 4 utilized only drought avoidance mechanism. In the current study, stomata closure, deeper roots and early maturity are traits associated with the identified drought adaptation mechanisms. Low temperatures affected bambara groundnut landraces. Further studies are suggested to investigate and screen a large collection of bambara groundnut landraces and genotypes under low temperature conditions. Because of the drought resistance ability shown by the two legumes, both can be cultivated in dry areas. Furthermore, the two species are suitable for crop diversification and intensification with higher chances of offering yields under drought conditions, which is one of the projected effects of climate change. In the present study, it was difficult to investigate some key drought stress related traits under field conditions. Further studies were conducted under rain out shelter conditions to explore both above and below ground drought related parameters. These studies are presented in Chapters 5 and 6.

CHAPTER FIVE

Responses of Above Ground Parameters of Bambara Groundnut (*Vigna subterranea* (L.)) and Groundnut (*Arachis hypogaea* (L.)) to Imposed Soil Water Deficit Stress at Different Growth Stages

5.1 Introduction

Drought is a major crop production constraint worldwide, occurring on all continents with varying intensity and frequency with considerable crop yield reductions. It is estimated that crop cultivation on the earth is only possible on 16% of the potentially arable area due to limited availability of water (Alexandratos and Bruinsma, 2012). Drought affects nearly all plant growth processes (Farooq et al., 2009; Praba et al., 2009); though, the influence of stress depends on factors like; intensity, rate, period and stage of plant growth (Demirevska et al., 2009). The effect of limited water supply on the plant growth processes has been extensively reported (Sazares et al., 2011; Vurayai et al., 2011a; Muhammad et al., 2015). For example, water deficit stress reduced photosynthesis due to stomatal closure in sunflower (*Helianthus*) (Cechin et al., 2006), bambara groundnut (*Vigna subterranea* (L.) Verdc) (Jorgensen et al., 2011; Muhammad et al., 2015), groundnut (*Arachis hypogaea* (L.)) (Songsri et al., 2013).

Closing of stomata assists in preserving relative leaf water content, thus higher leaf water status, however in expense of photosynthesis, plant biomass and crop yield. Various plant stresses have resulted to accumulation of compatible solutes like proline, which has been reported as an important trait in resistance strategy against drought (Padimavaghi and Rao, 2013). Proline possesses properties of antioxidant and it functions as an osmoprotectant as well as redox-buffering molecule especially during different stress conditions (KaviKishor and Sreenivasulu, 2014). Proline build up in water limited conditions has been evident in several

plants, for instance in bambara groundnut (Vurayai et al. (2011a); Muhammad et al. (2015), in groundnut (Sharada and Naik, 2011; Vaidya et al., 2015) and in black gram (*Vigna mungo*), green gram (*Vigna radiata*) (Baroowa and Goigoi, 2012). Legumes are generally resistant to drought but there are known differences between species and varieties (Daryanto et al., 2015). In soil water deficit experiments, Daryanto et al. (2015) revealed that, lentil (*Lens culinaris* Medikus) and groundnut exhibited lower yield reduction as compared to faba bean (*Vicia faba* (L.)). An experiment by Kumaga et al. (2003), showed that, soil water deficit stress significantly reduced growth of both cowpea and bambara groundnut but not groundnut.

Today still contradictory statements exist about the drought resistance of bambara groundnut and groundnut. Bambara groundnut is considered as the most drought resistant of the grain legumes (Tweneboah, 2000; Mazahib et al., 2013) with great potential as an alternative legume to groundnut and soybean (*Glycine max* L.), which cannot withstand harsh agronomic conditions (Mazahib et al., 2013). However, Kumaga et al. (2003) reported groundnut as a better performer than bambara groundnut under drought conditions. In an experiment by de Lima Pereira et al. (2016), earliness and upright growth habit were identified as key traits in a drought resistant groundnut line and recommended the line for cultivation in semi-arid environments. Further drought related investigations need to be carried out to compare the two legume species. This will ascertain individual species' drought resistance ability and hence their possible utilization in mitigating climate change and improving crop yields in drought prone areas.

Bambara groundnut cultivation is mainly dependent on landraces, which are uncharacterized, under-researched, and underutilised (Adegbola and Bamishaiye, 2011; Mabhaudhi et al., 2013). Additionally, the drought resistance mechanisms that permit bambara groundnut

cultivation in dry areas have not been fully elucidated (Inuwa and Muhammad, 2017). Similarly, limited information is available to support its drought resistance superiority over its comparator, groundnut. The objective of the present study was to determine the physiological effects of soil water-deficit stress on bambara groundnut and groundnut as assessed by leaf proline accumulation, gas exchange, chlorophyll content index and relative leaf water content. The outcome will not only further our understanding of drought response mechanisms in these two species but will also provide comparative evidence on the adaptability of the two species to semi-arid environments.

5.2 Materials and Methods

Details for all materials and methods are as described in chapter 3 section 3.7

5.3 Results

5.3.1 Soil characteristics

The soil characterization was performed prior starting of the experiments. The soil chemical and physical properties are presented in *Table 5.3.1*.The soil textural class during two seasons was loamy sand.

Table 5.3.1: Chemical and Physical properties of the soil used in the experiment at the University of Nottingham Malaysia Campus rainout shelter between 2017 and 2018 cropping seasons.

Soil Characteristics		Season	
		2017	2018
Soil pH (1:2.5) in H20		5.02	5.06
Particle size analysis	% Clay	14.32	14.40
	% Silt	2.90	3.00
	% Sand	82.78	82.86
	Textural class	Loamy sand	Loamy sand
Total Nitrogen (%) (K		0.06	0.06
Organic Carbon (%)		0.54	0.55
Acid Fluoride Soluble P (mg/kg)		8.74	8.73
Cation Exchange Capacity (Cmol/kg)		5.33	5.34
Exchangeable Bases (cmol/kg)	Ca2+	2.32	2.31
	Mg2+	0.43	0.44
	K+	0.19	0.20

5.3.2 Environmental conditions

The environmental conditions recorded during the trial period included photosynthetically active radiation (PAR), maximum and minimum daily temperatures and relative humidity (*Figure 5.3.1*). Weather data recorded over the two seasons (2017 and 2018) showed no significant ($P > 0.05$) differences in all parameters (*Figure 5.3.1*). Mean daily temperatures were in a range of 29 – 41 ^{o}C and 22 – 26 ^{o}C for maximum and minimum temperatures respectively.

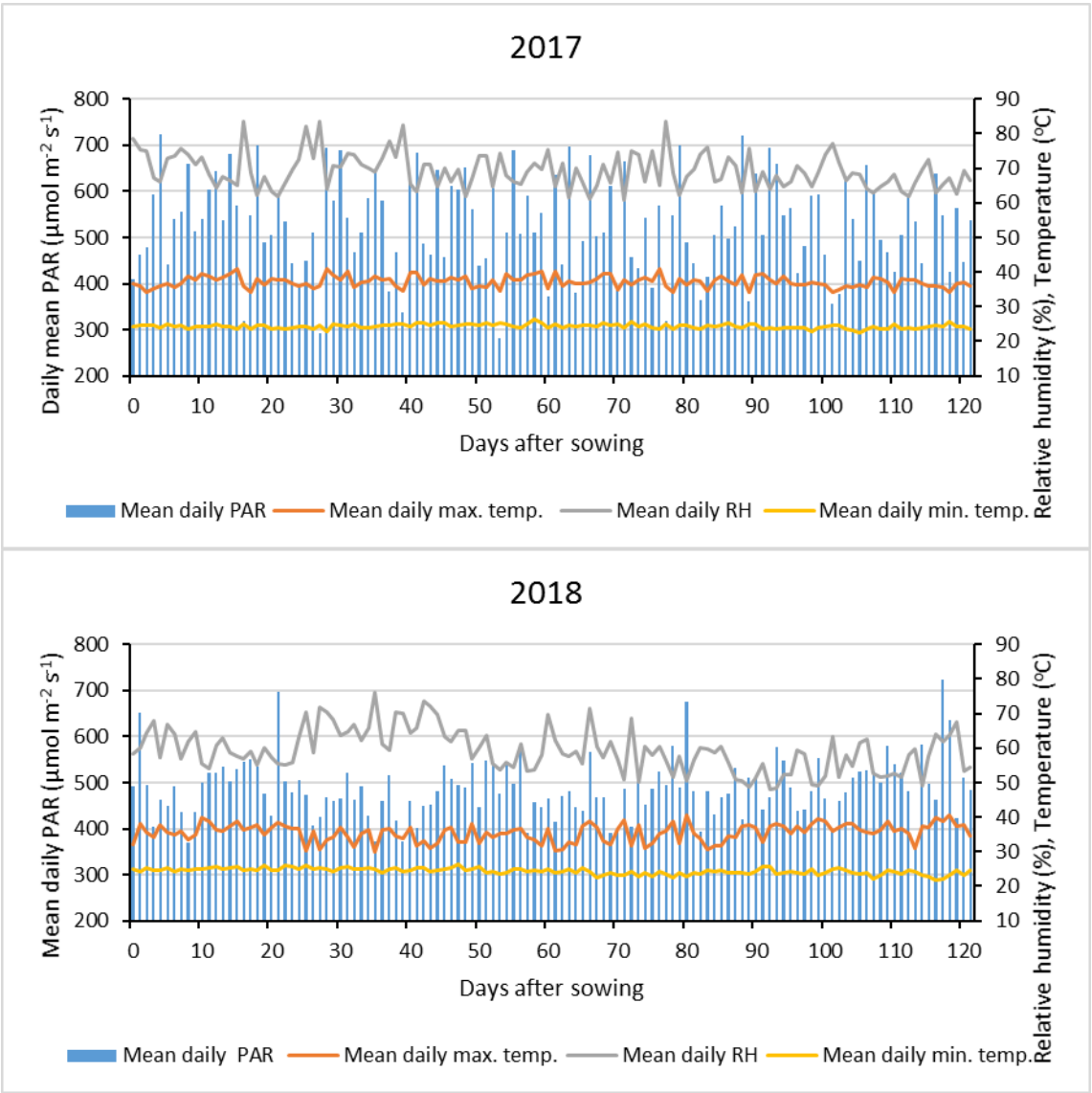


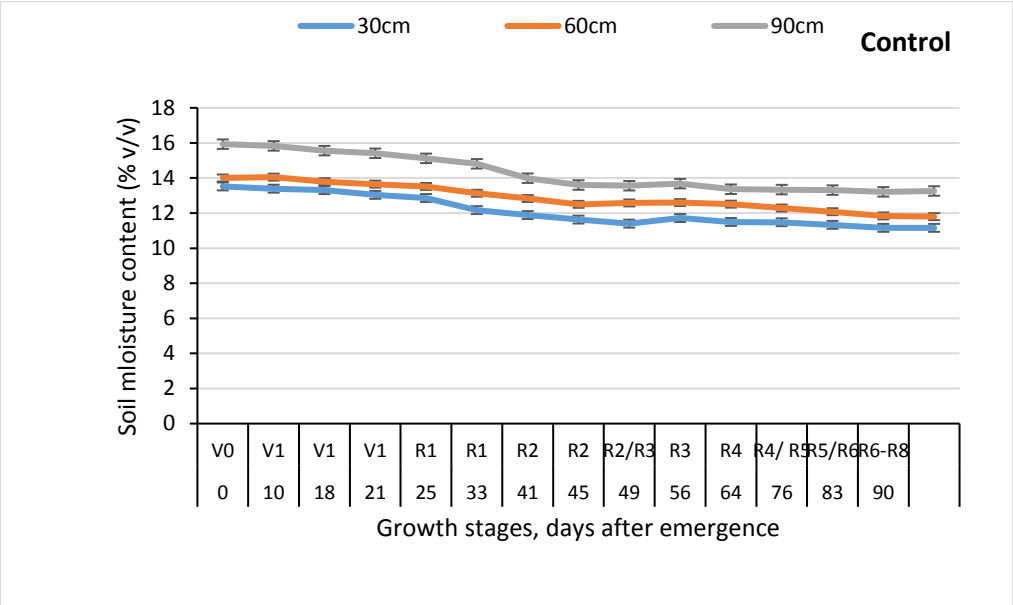
Figure 5.3.1: Variations in weather parameters i.e. Photo synthetically active radiation (PAR), relative humidity (RH), maximum and minimum temperatures during 2017 and 2018 seasons at the University of Nottingham rain outer shelter, Malaysia.

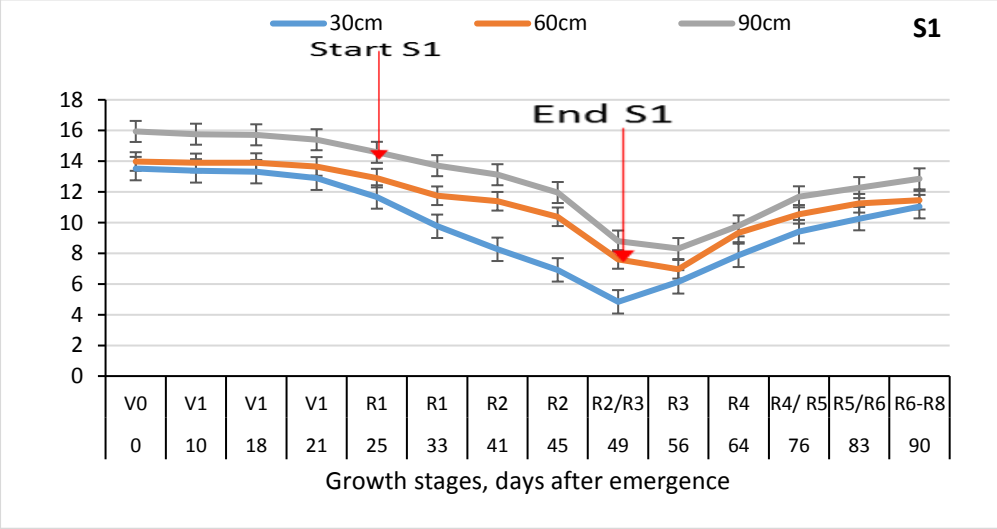
5.3.3 Combined Analysis of Variance (ANOVA)

Separate analysis of variance showed significant ($p < 0.05$) effects of the landraces, water regimes and their interactions for the studied traits. Test for homogeneity of variances between two years showed no significant ($p > 0.05$) differences, hence combined analysis of variance was performed. The results for the combined ANOVA are presented in the *Appendix 1* and *Appendix 2.* Years differed significantly only for proline content ($p = 0.026$) during flowering and stomatal conductance ($p = 0.013$) during pod development. Interactions between years and water regimes were only significant ($p < 0.05$) for proline during flowering (*Appendix 1*), photosynthetic rate and stomatal conductance during pod development (*Appendix 2*). The interactions between years and landraces were significant ($p < 0.05$) only during flowering for photosynthetic rate and only during pod development for stomatal conductance (*Appendix 2*). The interactions between year, water regimes and landraces were only significant for relative water content ($p = 0.01$) during flowering (*Appendix 1*) and chlorophyll content index ($p = 0.018$) during pod development. The current investigation revealed that, years had less effect on the studied parameters. This implies that, water deficit stress and plant materials are the main contributors for the differences observed during the growth stages.

5.3.4 Soil moisture content

The volumetric water content of the well-watered columns did not change significantly ($p > 0.05$) throughout the experimental period but decreased with the plants' development (


30cm
60cm
90cm
Control
Soil mloisture content (% v/v)
18
16
14
12
10
8
6
4
2
0
V0 V1 V1 V1 R1 R1 R2 R2 R2/R3 R3 R4 R4/ R5 R5/R6 R6-R8
0 10 18 21 25 33 41 45 49 56 64 76 83 90
Growth stages, days after emergence


30cm
60cm
90cm
S1
Start S1
End S1
18
16
14
12
10
8
6
4
2
0
V0 V1 V1 V1 R1 R1 R2 R2 R2/R3 R3 R4 R4/ R5 R5/R6 R6-R8
0 10 18 21 25 33 41 45 49 56 64 76 83 90
Growth stages, days after emergence

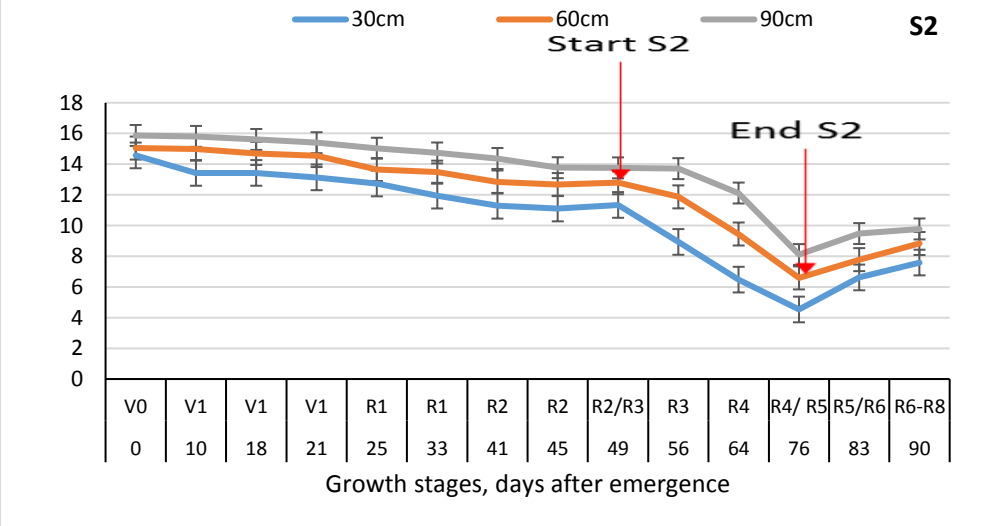
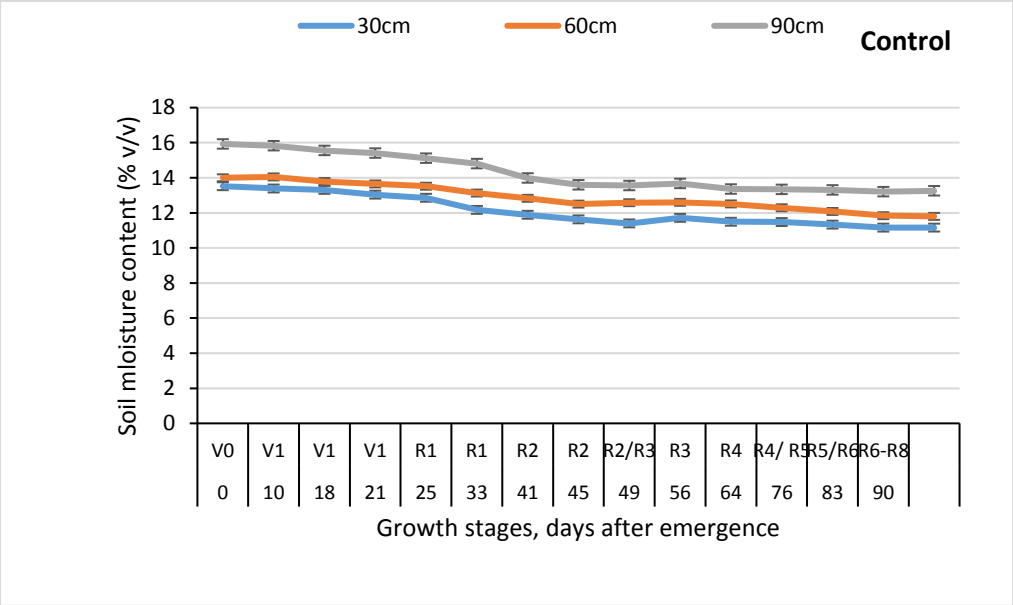
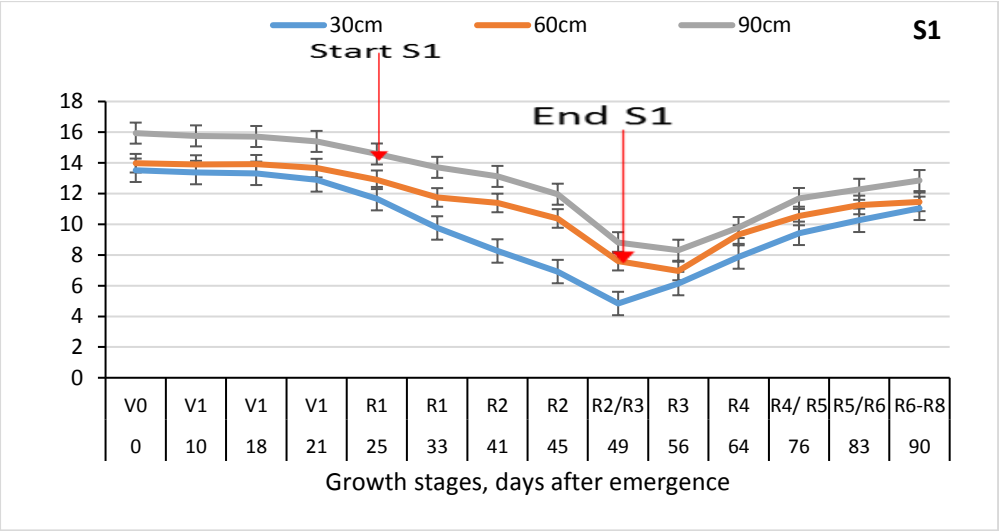
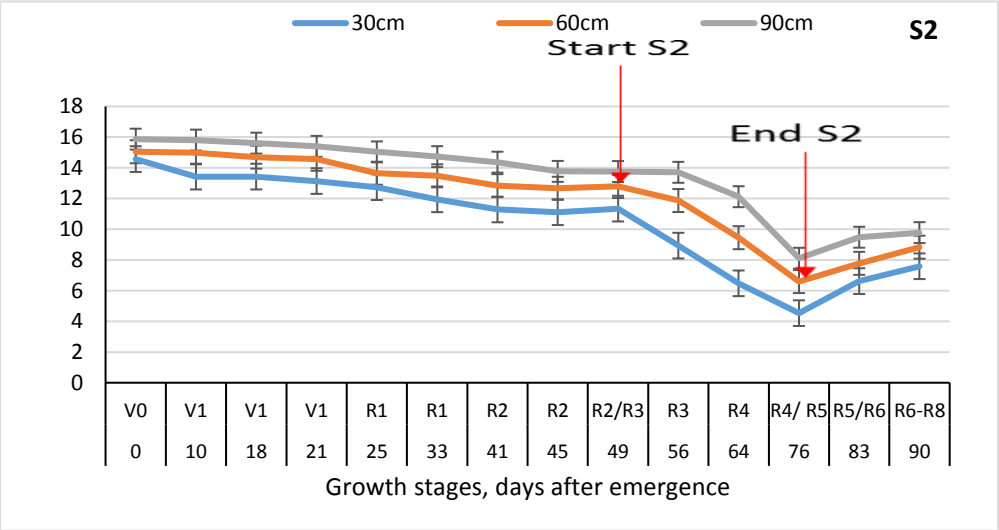

30cm
60cm
90cm
S2
Start S2
End S2
18
16
14
12
10
8
6
4
2
0
V0 V1 V1 V1 R1 R1 R2 R2 R2/R3 R3 R4 R4/ R5 R5/R6 R6-R8
0 10 18 21 25 33 41 45 49 56 64 76 83 90
Growth stages, days after emergence

Figure 5.3.2*).* In both water deficit stressed treatments the volumetric water content gradually declined. During water deficit stress at flowering stage, volumetric soil moisture (at 90 cm depth) in well-watered plants was 13.56% whereas in the stressed plots the soil moisture content dropped to 8.5 %. The soil moisture content at the end of stress during pod development was 12.57 % for control plots and 4.22 % for water deficit stressed plots (




30cm
60cm
90cm
S1
Start S1
End S1
18
16
14
12
10
8
6
4
2
0
V0 V1 V1 V1 R1 R1 R2 R2 R2/R3 R3 R4 R4/ R5 R5/R6 R6-R8
0 10 18 21 25 33 41 45 49 56 64 76 83 90
Growth stages, days after emergence


30cm
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S2
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End S2
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V0 V1 V1 V1 R1 R1 R2 R2 R2/R3 R3 R4 R4/ R5 R5/R6 R6-R8
0 10 18 21 25 33 41 45 49 56 64 76 83 90
Growth stages, days after emergence

Figure 5.3.2).

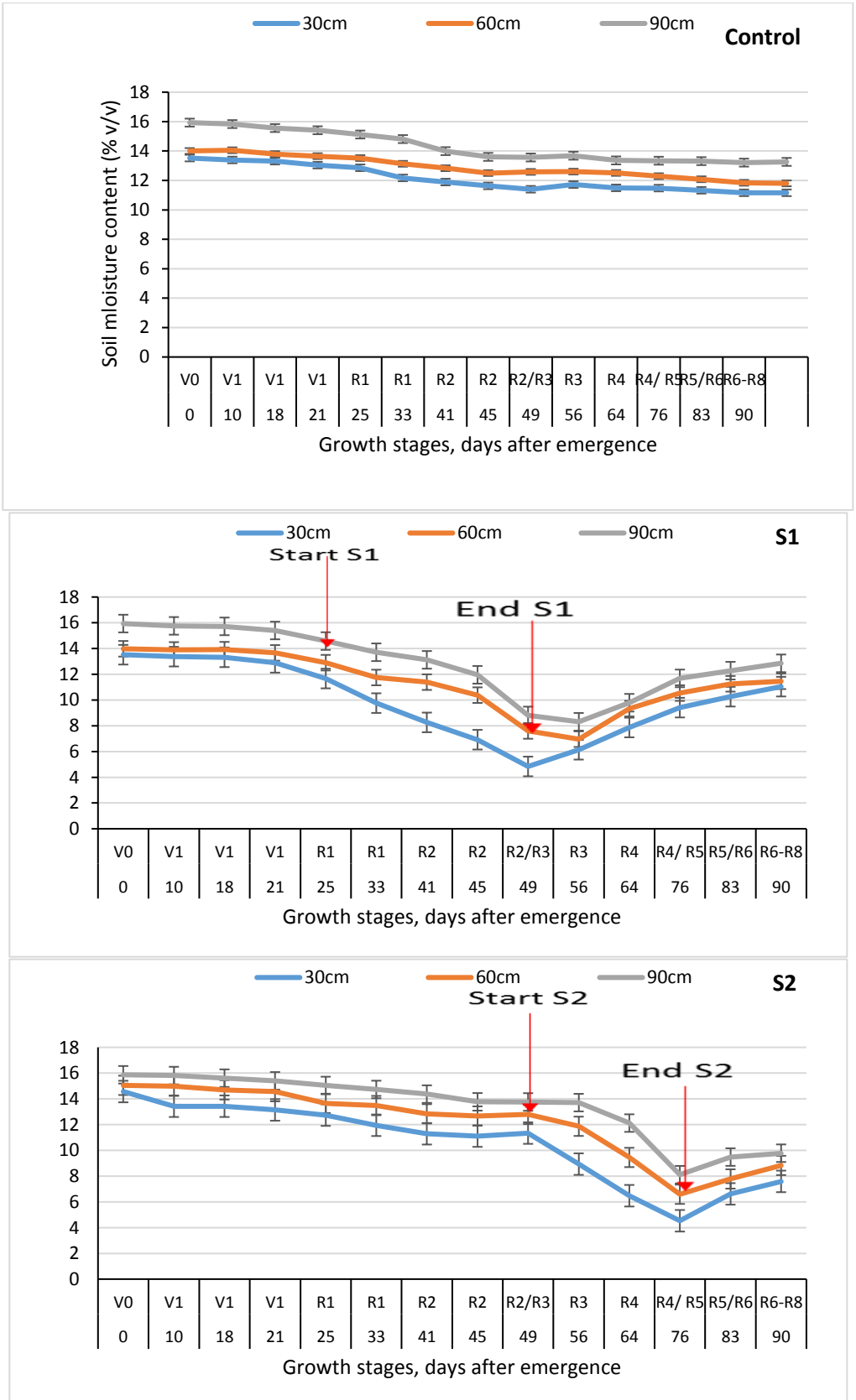


Figure 5.3.2: Variations in soil moisture content in different water stress regimes at different soil depths (30 cm, 60 cm and 90 cm) during 2018 cropping season in rain out shelter experiment. Control = well-watered through, S1 = Water deficit stress during flowering, S2 = Water deficit stress during pod development, V = vegetative, R1 = Beginning of bloom, R2 = Beginning peg, R3 =Beginning pod, R4 = Full pod, R5 = Beginning seed, R6 - R8 = Maturity. (n = 6).

5.3.5 Physiological and crop development traits

Water use efficiency (WUE)

Results for combined analysis of WUE are presented in *Table 5.3.2.* Significant ($p < 0.001$) differences in WUE were observed due to water deficit stress. Water deficit stress during flowering had more effect than during pod development. Water deficit stress increased WUE in bambara groundnut landraces. Significant ($p < 0.001$) differences existed among the bambara groundnut landraces. Interaction between water regimes and bambara groundnut landraces was also significant ($p < 0.001$) (*Table 5.3.2*).

Table 5.3.2: Combined effects of soil water deficit stress on water use efficiency (WUE) on bambara groundnut and groundnut during 2017 and 2018 seasons under rainout shelter experiments at University of Nottingham Malaysia Campus.

Treatments		WUE (kg m^{-3})	% Δ
Water regimes	Control	0.74^{c}	
	Flowering stress	0.88^{a}	19
	Podding stress	0.85^{b}	15
Landraces	DodR	0.66^{b}	
	NALBAM 4	0.65^{b}	
	S19-3	1.16^{a}	
	MNANJE	1.074	
Interaction			
DodR	Control	$0.63e^{f}$	
	S1	0.69^{d}	10
	S2	0.66^{de}	5
NALBAM 4	Control	0.59^{f}	
	S1	0.69^{d}	18
	S2	0.68^{d}	16
S19-3	Control	1.01^{c}	
	S1	1.27^{a}	25
	S2	1.21^{b}	19
Water regimes	*p-value*	<.001	
Landraces	*p-value*	<.001	
Interaction	*p-value*	<.001	
MNANJE	Control	1.307^{a}	
	S1	1.006^{b}	-23
	S2	0.909^{c}	-30
	p-value	<.001	

Values followed by the same superscript are not significantly different according to Duncan's Multiple Range Test. WUE = water use efficiency, % Δ = percentage change with respect to control. S1 = stress during floering, S2 = stress during pod development, Analysis of variance was done separately for each species. (n = 6).

Neither interaction between landrace and year, water regime and year nor interaction between water regime, landrace and year showed significant ($p > 0.05$) differences (*Appendix 2*). Landrace S19-3 gave the highest WUE values in all water regimes followed by DodR, although there was no significant differences between DodR and NALBAM 4. Higher percentage changes in WUE was found in S19-3 followed by NALBAM 4 and DodR. MNANJE outweighed DodR and NALBAM 4 in WUE but was inferior to S19-3 (*Table 5.3.2*). Different to bambara groundnut, water deficit stress significantly ($p < 0.001$) decreased WUE in MNANJE. Furthermore, MNANJE showed the highest percentage change in WUE in both water deficit stress periods. As opposed to bambara groundnut landraces, MNANJE was more affected during pod development.

Crop phenology

Figure 5.3.3 presents the results for duration taken to complete different growth stages of bambara groundnut and groundnut landraces under the study. Water deficit stress had no significant ($p > 0.05$) differences in either of the growth stages studied. Significant differences ($p < 0.001$) existed between the bambara groundnut landraces. There was no significant ($p > 0.05$) difference observed between the bambara groundnut landraces on days to emergence. However, highly significant ($p < 0.001$) differences existed in all other assessed growth stages. Among the bambara groundnut landraces, S19-3 took the least number of days to complete different growth stages (*Figure 5.3.3*). Days to flowering were 33, 36 and 38 for S19-3, DodR and NALBAM 4 respectively. Although it is known that, groundnut emerges earlier than bambara groundnut, in this case MNANJE was sown three days after bambara groundnut landraces in order to synchronize days to emergence between the two species. It can be noticed that, MNANJE had the shortest days for all other growth stages as compared to bambara groundnut landraces (*Figure 5.3.3*).

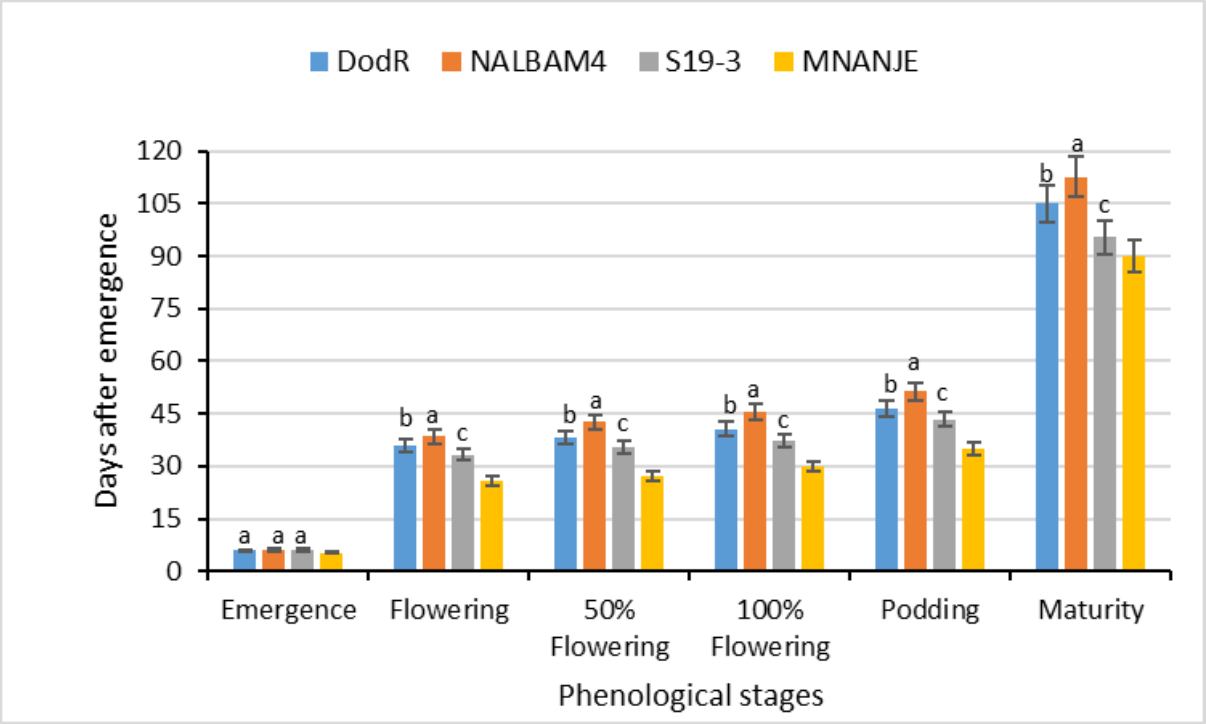


Figure 5.3.3: Two seasons (2017 and 2018) mean effects of water deficit stress on phenological stages of bambara groundnut (DodR, NALBAM 4, S19-3) and groundnut (MNANJE) landraces. Mean separations are for bambara groundnut landraces only, groundnut (MNANJE) was analysed separate. (n = 6).

Leaf proline

Highly significance differences ($p < 0.001$) existed among bambara groundnut landraces and between water regimes. Interaction between water regimes and bambara groundnut landraces was significant at ($p < 0.001$). Among interactions with years, only water regimes and years showed significant ($p = 0.003$) difference (*Appendix 1*). Proline accumulated under both water-deficit treatments (*Figure 5.3.4*). The highest percentage increase in proline from the control was found during flowering period. Among bambara groundnut landraces, S19 – 3 accumulated the highest leaf proline (150%) followed by DodR (120%) and NALBAM 4 (89%). Among water regimes, water stressed plants had 121% increase during flowering and 103% during pod development as compared to control plants. Although groundnut (MNANJE) was analysed separately, it showed the same trend as for bambara groundnut landraces but with higher proline content values. Higher percentage increase in proline content was found in

MNANJE plants droughted during flowering (174%) as compared to percentage proline increase during pod development (113%).

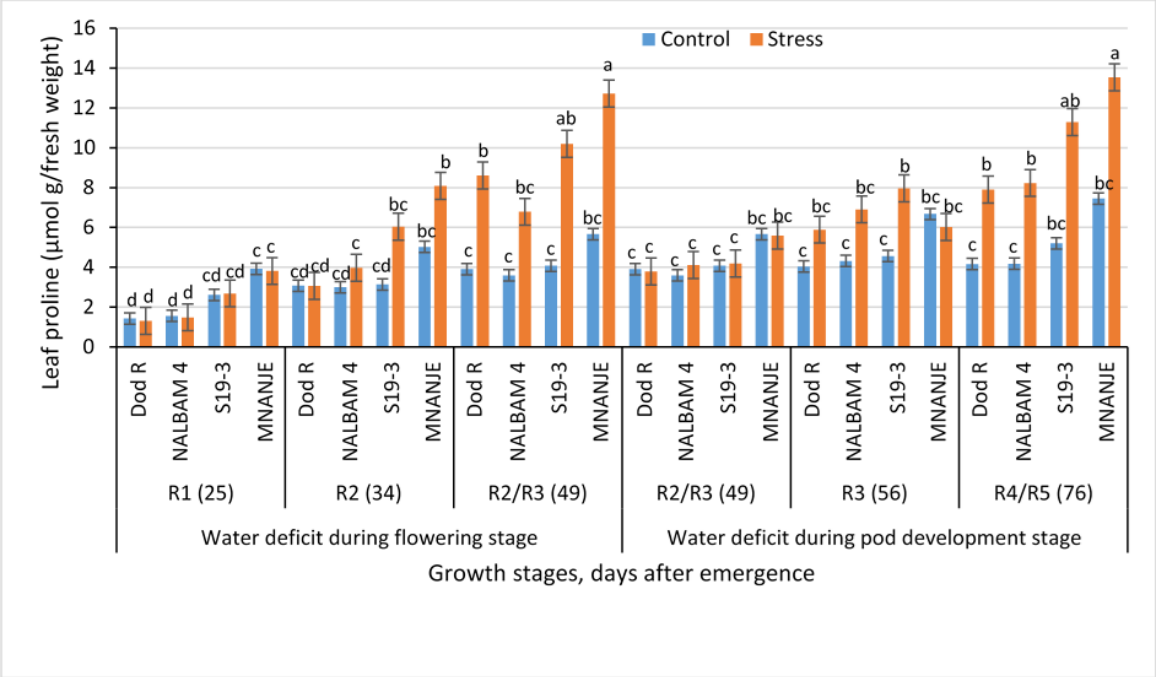


Figure 5.3.4: Combined mean leaf proline content (µmol g/fresh weight) of well-watered and drought stress treatments of bambara groundnut and groundnut (MNANJE) landraces during flowering and pod development stages in two consecutive seasons (2017 and 2018). Groundnut landrace (MNANJE) was analysed separately, R2 = Beginning peg, R3 =Beginning pod, R4 = Full pod, R5 = Beginning seed. (n = 12).

Gaseous exchange

As shown in *Table 5.3.3* photosynthesis rate (P_N), stomatal conductance (gs) and transpiration rate (E) were reduced under water deficit in the bambara groundnut and groundnut landraces. The P_N, gs and E were significantly lower ($p < 0.001$) in water stressed plants both during flowering and pod development. The effect of water deficit stress was higher in plants stressed during flowering. Bambara groundnut landraces differed significantly ($p < 0.001$) in P_N, g_s and E. Interaction between water regimes (WR) and landraces (L) revealed significant ($p < 0.001$) differences. Higher gas exchange values and lower percentage changes in bambara groundnut landraces were evident in S19 – 3 than in the other bambara groundnut landraces (*Table 5.3.3*). Nevertheless, groundnut (MNANJE) gave the highest values of P_N, gs and E coupled with lowest percentage changes between the control and the stressed plants.

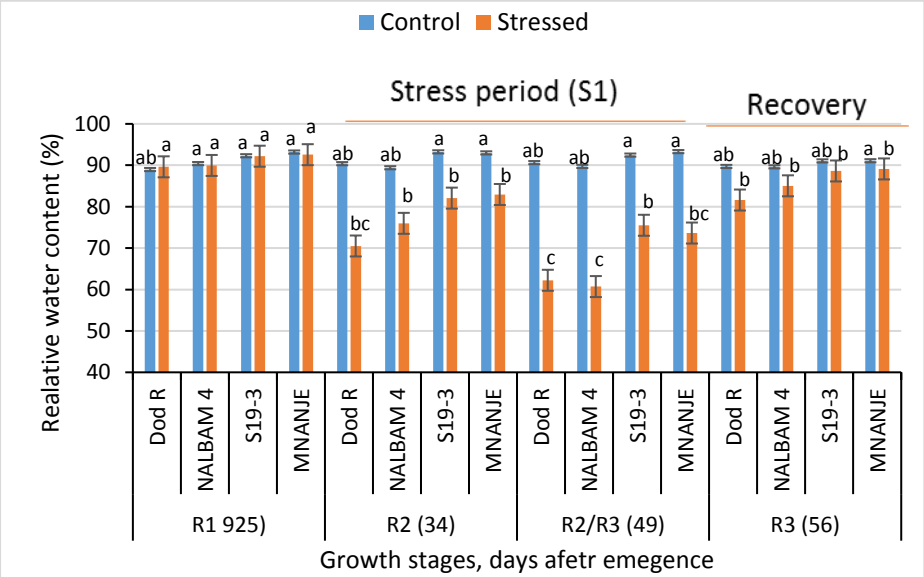
Table 5.3.3: The mean changes in Photosynthetic rate (PN -µmol CO_2 m^{-2} s^{-1}), Stomatal conductance (gs -H_20 mol m^{-2} s^{-1}) and Transpiration (E - H_20 mol m^{-2} s^{-1}) of bambara groundnut (DodR, NALBAM 4, S19-3) and groundnut (MNANJE) landraces in rain out shelter experiments at Nottingham University Malaysia Campus under water deficit stress during flowering and pod development stages for two consecutive years (2017 and 2018).

		Photosynthesis rate				Stomatal conductance				Transpiration rate			
		S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ
Water regimes	Control	70.41^{a}		45.87^{a}		1.97^{a}		0.38^{a}		18.68^{b}		4.46^{a}	
	Stressed	13.30^{b}	-81	11.80^{c}	-74	0.20^{b}	-90	0.14^{c}	-64	3.37^{c}	-82	1.88^{b}	-58
	p-value	<.001		<.001		<.001		<.001		<.001		<.001	
Landraces	DodR	53.44^{b}		31.41^{b}		1.39^{b}		0.20b		11.65^{c}		2.71^{c}	
	NALBAM 4	39.60^{c}		16.57^{c}		0.67^{c}		0.17^{c}		14.95^{b}		3.13^{b}	
	S19-3	60.86^{a}		43.97^{a}		2.03^{a}		0.36^{a}		16.02^{a}		4.89^{a}	
	p-value	<.001		<.001		<.001		<.001		<.001		<.001	
	MNANJE	108		32.88		2.8		0.29		18.1		4.6	
Landrace x Water regime													
DodR	Control	74.72^{bc}		39.03^{c}		1.99^{b}		0.43^{a}		14.38^{c}		3.91b^{c}	
	Stressed	11.07^{f}	-85	12.17^{e}	-69	0.19^{d}	-90	0.04^{e}	-90	2.94^{d}	-84	1.04^{e}	-73
NALBAM 4	Control	54.89^{d}		23.34^{d}		0.99^{c}		0.27^{c}		18.73^{b}		3.80b^{c}	
	Stressed	9.48^{f}	-83	4.08^{f}	-83	0.11^{d}	-89	0.08^{e}	-69	2.04^{d}	-88	1.64^{e}	-57
S19-3	Control	81.64^{a}		45.23^{c}		2.96^{a}		0.45^{a}		21.93^{a}		5.68^{a}	
	Stressed	19.35^{e}	-76	17.15^{e}	-62	0.37^{d}	-88	0.29^{c}	-37	4.13^{d}	-81	2.97^{d}	-48
	p-value	<.001		<.001		<.001		<.001		<.001		<.001	
MNANJE	Control	147.00^{a}		49.93^{a}		3.03^{a}		0.37^{a}		23.06^{a}		5.57^{a}	
	Stressed	35.10^{b}	-76	20.15^{c}	-60	0.44^{b}	-86	0.24^{b}	-34	4.95^{b}	-79	3.02^{b}	-46
	p-value	<.001		<.001		<.001		<.001		<.001		<.001	

Values followed by the same superscript are not significantly different according to Duncan's Multiple Range Test (DMRT). % Δ = percentage change with respect to control. Groundnut (MNANJE) landrace was used just for comparison. Analysis of variance was done separately for each species. Bambara groundnut (n = 12).

Relative water content (RWC) (%)

Separate analysis of variance showed significant ($P < 0.05$) effects of the landraces, water regimes and their interactions for RWC in both years (there was no significant differences observed between the two years), hence, combined analysis of variance was carried out. Combined analysis of variance results for RWC are presented in *Appendix 1*. Stressing bambara groundnut and groundnut significantly ($p < 0.001$) reduced RWC compared to the control plants at both flowering and pod development stages (



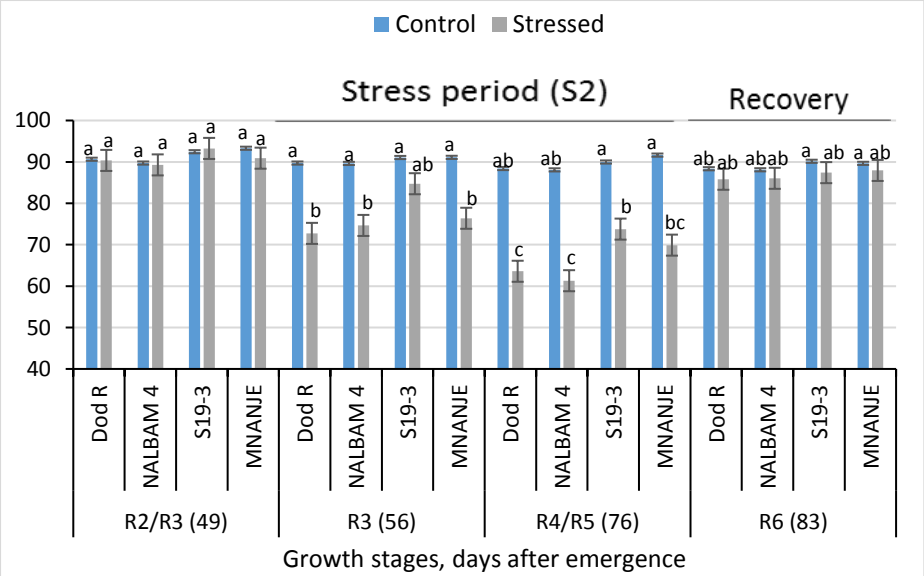
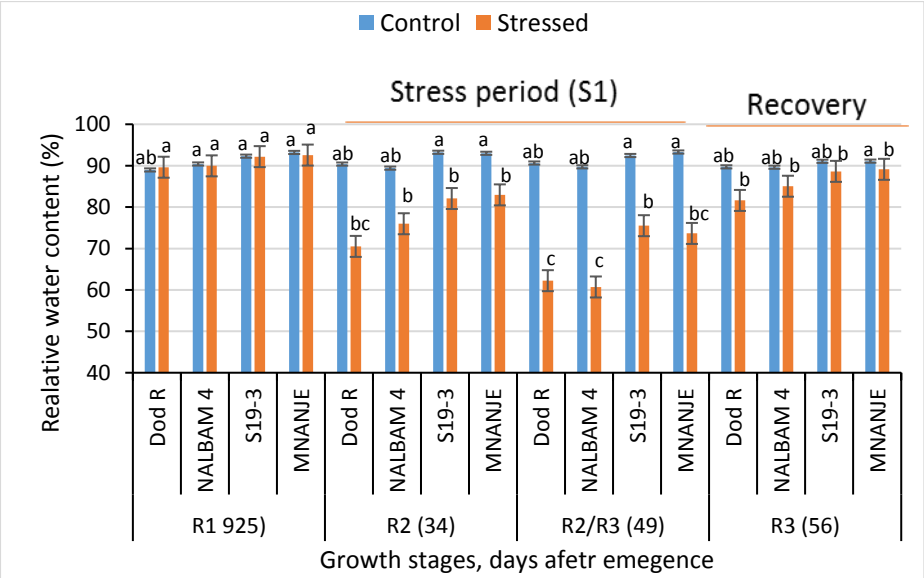


Figure 5.3.5). Landraces significantly ($p < 0.001$) differed in maintenance of RWC. Years did not significantly ($p > 0.05$) differ in RWC (*Appendix 1*). Similarly, the interaction between landraces and watering regimes was also significant ($p < 0.001$). Neither interaction between water regimes and years; landraces and years nor interaction between landraces, water regimes and years showed significant ($p > 0.05$) differences on RWC. In both species, higher percentage changes were found in plants stressed during flowering than in plants stressed during pod development. Relative water content decreased with time after imposition of water deficit stress. The decrease was significant ($p < 0.001$) in all bambara groundnut and groundnut landraces compared with the control. After seven days recovery, there was significant ($p < 0.05$) increase in relative leaf water content in all bambara groundnut landraces, with the highest levels observed in S19-3. MNANJE, the comparator, had the highest values in all water regimes as compared to individual bambara groundnut landraces (



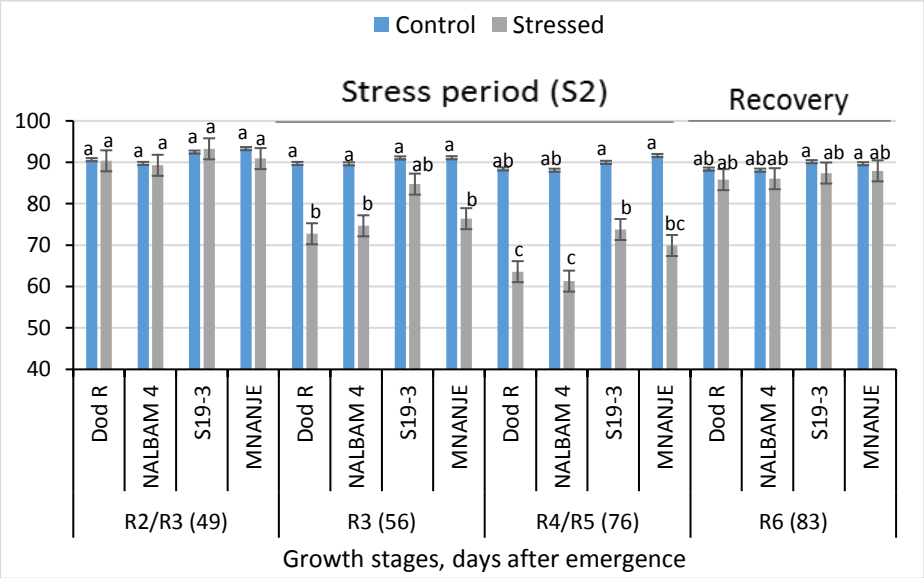


Figure 5.3.5). In addition, lowest percentage changes between stressed and control plants were observed in MNANJE.

Chlorophyll content index

The results of chlorophyll content index for bambara groundnut and groundnut landraces are shown in *Figure 5.3.6*. Both watering regimes and landraces showed significant differences ($p < 0.001$) (*Figure 5.3.6.*). The interaction between landraces and watering regimes was also significant ($p < 0.001$). The only interaction with years which showed significant ($p < 0.05$)

difference was between water regimes, landraces and years (*Appendix 1*). Other interactions did not show significant ($p > 0.05$) differences.

Among bambara groundnut landraces, chlorophyll content index values were generally higher in S19-3 than in DodR and NALBAM 4 landraces. The chlorophyll content index values obtained in all stressed bambara landraces were lower compared to the respective control plants. Chlorophyll content index was significantly ($p < 0.001$) lower in NALBAM 4 during both flowering and pod development stress periods. Although S19–3 outperformed the other two bambara groundnut landraces, its chlorophyll content index values were lower than the values of the comparator groundnut (MNANJE) (*Figure 5.3.6*). MNANJE showed significant ($p < 0.001$) increase in chlorophyll content values between the stressed plants and control in both water deficit stress periods (*Figure 5.3.6*).

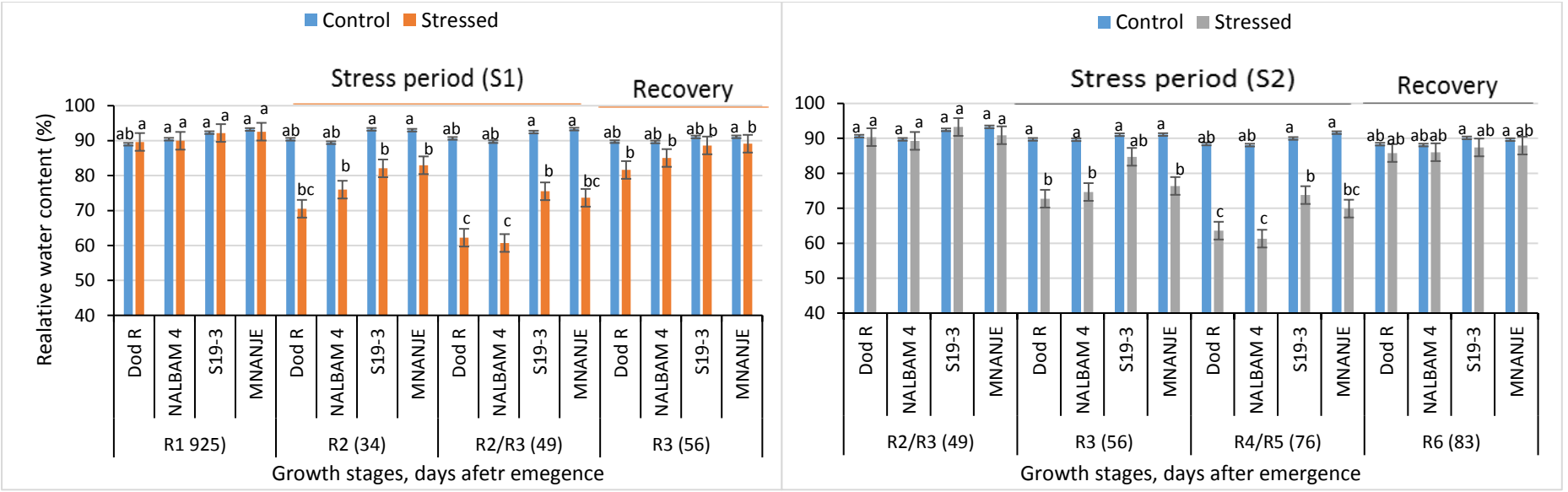


Figure 5.3.5: Combined mean relative water content (%) of bambara groundnut (DodR, NALBAM 4, S19-3) and groundnut (MNANJE) landraces under well irrigated (Control) and water deficit conditions during two consecutive seasons (2017 and 2018). (A), S1= water deficit stress during flowering, (B), S2 = water deficit stress during pod development, R1 = Flowering, R2 = Beginning peg, R3 =Beginning pod, R4 = Full pod, R5 = Beginning seed, R6 = Full seed (n = 12).

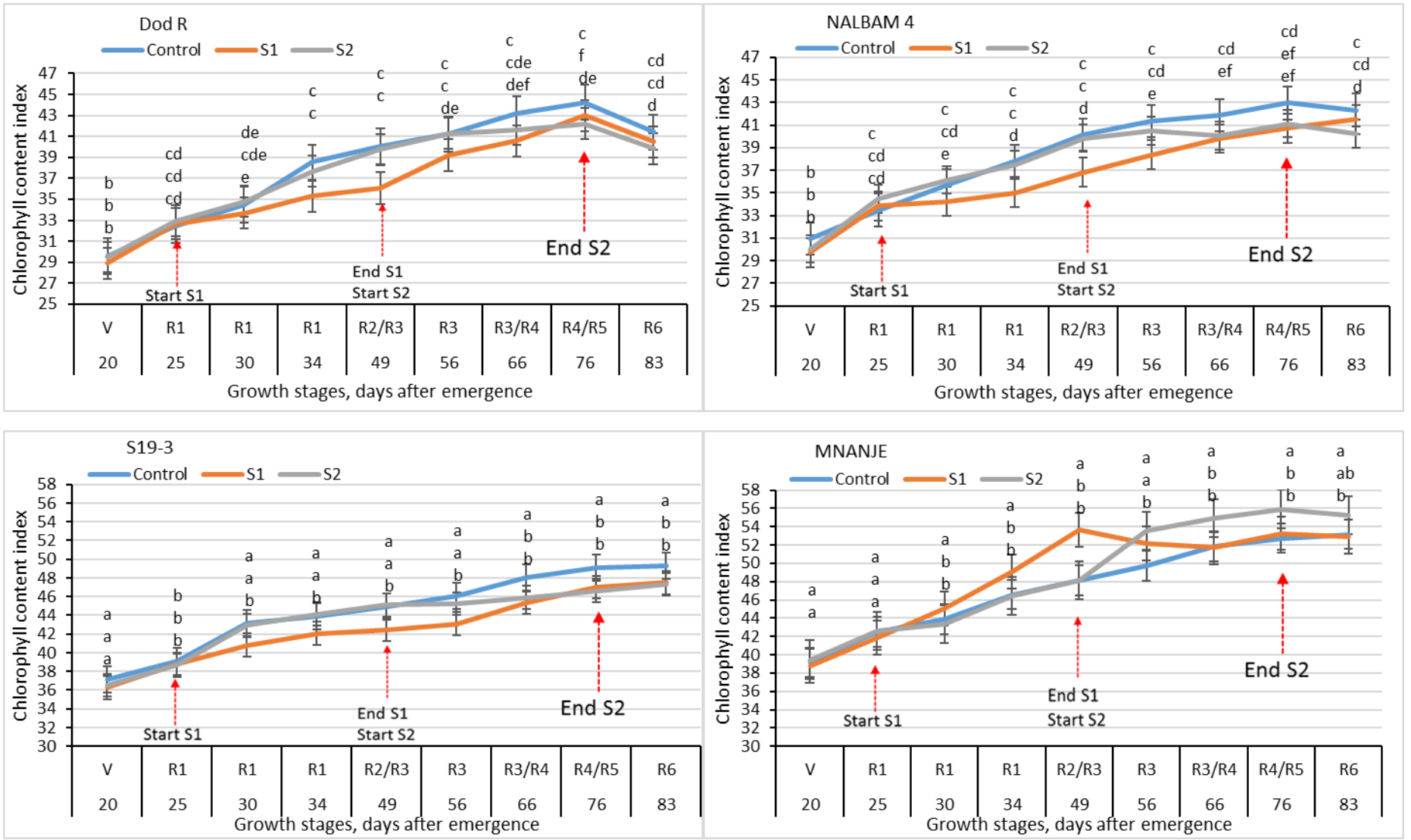


Figure 5.3.6: Combined mean chlorophyll content index of bambara groundnut (DodR, NALBAM 4, S19-3) and groundnut (MNANJE) landraces under well irrigated (Control) and water deficit conditions during two consecutive seasons (2017 and 2018) in a rain out shelter. S1= water deficit stress during flowering, S2 = water deficit stress during pod development, V = vegetative, R1 = Beginning of bloom, R2 = Beginning peg, R3 =Beginning pod, R4 = Full pod, R5 = Beginning seed, Full seed (n =18).

5.3.6 Yield components and yield

Table 5.3.4 presents the main effects of water regimes and landraces and interaction effects of water regimes and landraces on yield components and yield. Highly significant ($p < 0.001$) differences existed in all of the yield components between water regimes, landraces and their interaction. Final yield also revealed highly significant ($p < 0.001$) differences among the bambara groundnut landraces as well as between the water treatments and their interactions. Interaction between years, water regimes and landraces was not significant ($p > 0.05$) in the final grain yield. It must be noted that, as the experiments involved two different plant species, analysis of data was performed separately. Water deficit stress significantly ($p < 0.001$) reduced yield components and yield of groundnut (MNANJE). In both species, higher percent change (decrease) in number of pods per plant, pod weight (t ha^{-1}) and grain yield (t ha^{-1}) were found in plants stressed during flowering (S1) than in plants stressed during pod development (S2) (*Table 5.3.4*). In contrast, percent change in number of matured seeds per plant, a hundred seed weight and shelling percentage were more affected during the stress imposed during pod development. Among the bambara groundnut landraces, S19-3 revealed most of the lower changes in yield components. In addition, S19-3 showed the lowest percent change in the final yield. DodR and NALBAM 4 had low yields in all yield components and in most cases higher percentage changes (decrease) in yield components as compared to S19-3. With exception of number of pods and shelling percentage, MNANJE the comparator showed the lowest changes (decrease) in the other yield components and yield during both stress periods.

Table 5.3.4: Mean yield and yield components performance of bambara groundnut (DodR, NALBAM 4, S19-3) and groundnut (MNANJE) landraces in rain out shelter experiments at Nottingham University Malaysia Campus under water deficit stress during flowering and pod development stages for two consecutive years (2017 and 2018).

Treatments		Pods plant^{-1}	% change pods plant^{-1}	Dry pod weight plant^{-1}	Dry pod weight (t ha^{-1})	% change pod weight	Seeds plant^{-1}	% change seeds pant^{-1}	Seed weight plant^{-1} (g)	100 seed weight (g)	% change 100 seed weight	% Shelling	% change % shelling	Grain yield (t ha^{-1})	% change grain yield (t ha^{-1})
Water regimes	Control	40.22^{a}		31.08^{a}	2.51^{a}		41.44^{a}		22.57^{a}	46.02^{a}		73.02^{a}		1.88^{a}	
	S1	19.00^{c}	-53	14.10^{c}	1.12^{c}	-55	17.98^{c}	-57	8.94^{c}	40.58^{b}	-12	63.71^{b}	-13	0.72^{c}	-62
	S2	35.33^{b}	-12	24.27^{b}	2.02^{b}	-20	32.50^{b}	-22	10.13^{b}	30.16^{c}	-26	43.41^{c}	-32	0.88^{b}	-53
Landraces	DodR	23.06^{b}		18.20^{b}	1.51^{b}		23.93^{b}		11.45^{b}	42.25^{a}		59.11^{b}		0.93^{b}	
	NALBAM 4	19.44^{c}		18.09^{b}	1.36^{c}		19.50^{c}		11.29^{b}	37.92^{b}		63.29^{a}		0.96^{b}	
	S19-3	52.06^{a}		33.17^{a}	2.78^{a}		48.50^{a}		18.91^{a}	36.60^{b}		57.75^{b}		1.60^{a}	
	MNANJE	36.78		37.1	2.94		64.39		24.87	40.79		67.48		2.09	
Interaction															
Control	DodR	28.50^{c}		25.08^{c}	2.08^{c}		31.33^{c}		19.13^{b}	50.67^{a}		72.69^{a}		1.56^{b}	
	NALBAM 4	24.33^{d}		26.42^{c}	1.90^{d}		25.00^{d}		17.85^{c}	44.66^{b}		73.25^{a}		1.56^{b}	
	S19-3	67.83^{a}		41.75^{a}	3.56^{a}		68.00^{a}		30.74^{a}	42.72^{bc}		73.12^{a}		2.53^{a}	
S1	DodR	14.50^{f}	-49	11.50^{f}	0.73^{g}	-65	14.45^{f}	-54	7.04^{g}	41.90^{bc}	-17	62.23^{b}	-14	0.55^{f}	-65
	NALBAM 4	12.53^{f}	-48	11.79^{f}	0.64^{g}	-67	13.50^{f}	-46	7.83^{fg}	40.20^{c}	-10	65.97^{b}	-10	0.58^{ef}	-63
	S19-3	28.00^{cd}	-59	19.01^{d}	1.59^{e}	-55	26.00^{d}	-62	11.96^{e}	39.64^{c}	-7	62.94^{b}	-14	1.04^{d}	-59
S2	DodR	26.17^{cd}	-8	18.02d^{e}	1.52^{e}	-27	26.00^{d}	-17	8.19^{f}	34.17^{d}	-33	42.43^{d}	-42	0.68^{ef}	-56
	NALBAM 4	19.50^{e}	-20	16.05^{e}	1.35^{f}	-29	20.00^{e}	-20	8.20^{f}	28.89^{e}	-35	50.64^{c}	-31	0.72^{e}	-54
	S19-3	60.33^{b}	-11	38.76^{b}	3.19^{b}	-10	51.50^{b}	-24	14.02^{d}	27.43^{e}	-36	37.18^{e}	-49	1.25^{c}	-51
Water regime	p < 0.05	<.001		<.001	<.001		<.001		<.001	<.001		<.001		<.001	
Landrace	p < 0.05	<.001		<.001	<.001		<.001		<.001	<.001		<.001		<.001	
Interaction	p < 0.05	<.001		<.001	<.001		<.001		<.001	0.015		<.001		<.001	
Control	MNANJE	45.00^{a}		53.29^{a}	4.14^{a}		83.50^{a}		39.22^{a}	47.03^{a}		73.60^{a}		3.27^{a}	
S1		22.17^{b}	-51	21.24^{c}	1.89^{c}	-54	44.33^{c}	-47	16.03^{c}	40.85^{b}	-13	71.37^{a}	-3	1.47^{c}	-55
S2		43.17^{a}	-4	36.78^{b}	3.79^{b}	-8	70.33^{b}	-16	19.35^{b}	34.48^{c}	-27	55.88^{b}	-22	1.74^{b}	-47
	p < 0.05	<.001		<.001	<.001		<.001		<.001	0.001		<.001		<.001	

Values followed by the same superscript are not significantly different according to Duncan's Multiple Range Test (DMRT). S1 = water deficit stress during flowering, S2 = water deficit stress during pod development. Groundnut (MNANJE) landrace was used just for comparison. Analysis of variance was done separately for each species (n = 6).

5.4 Discussion

Crop phenology

Average days to emergence varied between 5 - 7 after sowing. This was earlier than the 7 - 9 days reported by Berchie et al. (2010), 9 – 12 days reported by Al Shareef (2010) and 7–14 days reported by Swanevelder (1998). The earliness in emergence of these landraces may have been contributed by either pre-sowing treatment of seeds (seeds were soaked in water overnight) or the high temperature experienced in the rain out shelter. The seeds were grown under rain out shelter where the temperature inside reached a maximum of 41^{o}C. During sowing, germination and emergence treatments were under normal irrigation and therefore water was not a limiting factor. Seed germination and emergence are important indicator of crop establishment, which was very similar among the landraces in the present study. This can be an indicator that when soil moisture is non-limiting factor, landrace is not an important factor in determining the success of crop establishment.

The present finding is supported by a study of Mwale (2005). The landrace S19-3 took significantly fewer days to attain flowering, 50% flowering, pod formation and maturity over DodR and NALBAM 4 (*Figure 5.3.3*). This implies that, the landraces under study could widely adapt to a range of environments providing opportunity for a wide cultivation of the crop (Berchie et al., 2010). On the other hand, MNANJE, the comparator, took the least number of days to attain all phenological stages. Plants that flower and mature earlier are more favoured in escaping drought. In this study, MNANJE and S19-3 flowered and matured earlier than DodR and NALBAM 4 under drought conditions. Hence, they might mitigate drought through escape mechanism to survive in dry environments. With the current climate change, MNANJE and

S19 - 3 are prime candidates for inclusion in breeding programmes targeting early maturing traits in both species.

Water use efficiency

Water use efficiency has been expressed in different ways depending on the purpose or objective of the study. It can be expressed as the ratio of total biomass or grain yield to water supply or evapotranspiration or transpiration on a daily or seasonal basis (Sinclair et al., 1984). Mabhaudhi et al. (2013) on a study of bambara groundnut seedlings expressed WUE as a ratio of biomass accumulation, expressed in total seedling biomass (g), to water added in mm. High WUE is largely a function of reduced water use and net improvement in plant production (Blum, 2005). In this study, water deficit stress increased WUE in all bambara groundnut landraces. This could be attributed to the size of the shoot and the partitioning of assimilates to the pods. S19 – 3 showed the smallest shoot biomass compared to other landraces (see chapter 6), and had the highest WUE in all water regimes. The current findings are in line with a study on bambara groundnut seedlings (Mabhaudhi et al., 2015), who suggested that, the increased WUE could be related to the drought avoidance strategies by reduced shoot size observed in the stressed seedlings.

Drought escape and avoidance mechanisms have been shown to contribute to high WUE in bambara groundnut (Jorgensen et al., 2010; Vurayai et al., 2011a; Mabhaudhi and Modi, 2013). More reports revealed that, water use efficiency increased with decreased water supply (Nageswara Rao et al., 1994; Chibarabada et al., 2015; Mabhaudhi et al., 2015). The observed reduced WUE in MNANJE under water deficit stress in this study, might have been contributed by the large biomass of the crop, as a higher portion of assimilates might have been allocated to leaves than in pods and seeds. Other reason for the observed reduced WUE

in MNANJE could be a failure of the pegs to penetrate the dry soil under water deficit stress. Collino et al. (2001) and Songrsi et al. (2009) both have reported similar results in groundnut.

Leaf proline

The higher amounts of proline were mostly observed in water stressed plots. This suggests that, the landraces, which accumulate high content of proline during water stress, are likely to be drought resistant (Laik and Doftling, 1985; Soni and Abdin, 2017). Higher proline accumulation in plants during water stress might be acting as an osmoprotectant and helping resistant landraces in maintaining higher RWC and leaf water potential (Nautiyal et al. 2002).

The present results are in agreement with findings reported by Vurayai et al. (2011a); Coupel-Ledru et al. (2014) in bambara groundnut and attributed to the variation in stomatal regulation in drought resistant and susceptible landraces. Osmotic adjustment (OA) is important in drought resistance because of its contribution to continual cell expansion (Wyn Jones and Gorham, 1983), stomatal and photosynthetic adjustments (Ludlow, 1980). OA implies lowering of osmotic potential because of accumulation of solutes in response to insufficient water or salinity (Turner and Jones, 1980). Drought related studies have been conducted to characterize the accumulation of proline, a compound known to contribute to the osmotic adjustment and tolerance of plants exposed to unfavourable environmental conditions (Heuer, 2010). Proline is thought to contribute to osmotic adjustment, detoxification of ROS, and protection of membrane integrity (Vendruscolo et al., 2007). Vendruscolo et al. (2007); KaviKishor and Sreenivasulu, (2014) reported that proline accumulation in stressed plants is a tolerance mechanism against oxidative stress and it is the main strategy of plants to avoid harmful effects of drought stress. Increases of proline due to drought stress has been reported in other studies (Serraj and Sinclair, 2002; Safarnejad, 2004;

Gomes et al., 2010; Shamsi, 2010; Da Costa et al., 2011). Reports have related proline metabolism to stress resistance, and proline accumulation has been suggested as a parameter for selection of plant species resistant to wilting or salinity (Lutts et al., 1999; Gibon et al., 2000).

In the present study, MNANJE (groundnut) accumulated the highest amount of proline during drought stress and therefore showed a superior capacity to withstand water stress compared to the three landraces of bambara groundnut (S19-3, DodR and NALBAM 4). The highest percentage increase in proline content during water deficit stress shown by MNANJE indicates its ability to withstand water deficit stress as compared to bambara groundnut. Drought resistance superiority of groundnut over bambara groundnut has also been reported by Kumaga et al. (2003). S19-3 being a drought resistant (Jorgensen et al., 2011) landrace was outperformed by MNANJE in terms of proline content and or accumulation, implying that MNANJE is a superior drought resistant landrace.

Gaseous exchange

Gas exchange parameters monitored include stomatal conductance, photosynthetic rate and transpiration rate. Lower values of gas exchange parameters were observed in water deficit stressed plants as compared to control plants. In initial stages of growth in all landraces, the gas exchange parameters increase with plant growth. As opposed to initial growth stages, at later growth stages, gas exchange parameters decreased with plant growth. Progressive declines in stomatal conductance, photosynthetic rate and transpiration rate were evident in all soil water deficit stressed plants. This is consistent with findings reported by Collinson et al. (1997); Vurayai et al. (2011a); Chai et al. (2016) in bambara groundnut, Lanna et al. (2016) in soybean and Neto et al. (2010) in groundnut. This implies that, the regulation of stomatal

closure for control of water loss could be one of the early events in bambara groundnut and groundnut in response to drought.

The higher values of percentage decrease in both species was observed during water deficit during flowering as compared to water deficit stress during pod development. Regardless of water regime, at the late stage of plant growth there was a continuous decrease in stomatal conductance, photosynthetic rate and transpiration. This implies that, these three parameters are not only affected by water stress, but also plant age. These three parameters are positively related, stomatal conductance being the main driving force. Under drought, plants close their stomata to minimise water loss by transpiration, thereby conserving tissue moisture. Generally, in plants the overriding factor determining transpiration, photosynthesis and stomata response to drought stress is soil water content (Ray and Sinclair 1998). This agrees with the results obtained in the current study, as there was continuous decline in these three parameters as soil water deficit stress progressed. Plants that tend to preserve water under drought are referred to as drought avoiding plants (Muhammad et al., 2015).

A study by Mafakheri et al. (2010) reveals that, transpiration and stomatal conductance decreased in plants when they were subjected to drought stress. Stomatal closure is the first response of plants to drought which restricts gas exchange between the atmosphere and the inside of the leaf. Plants grown under drought conditions have a lower stomatal conductance in order to conserve water (Mafakheri et al., 2010). Decrease in transpiration and stomatal conductance points to the possibility of a drought avoidance strategy (Muhammad and Massawe, 2015). Preserving water during drought is associated with stomatal closure and limits the amount of CO_2 required for photosynthesis. As a result, net photosynthesis will negatively be affected and hence economic yield. Drought avoidance mechanism traits alone

must not be given first priority in breeding programmes, as their contribution to economic yield is less important. This is because avoidance drought mechanisms are achieved in expense of crop yield.

Chlorophyll content index (CCI)

As it can be seen from the results, water deficit stress decreased chlorophyll content index in bambara groundnut landraces. The decrease observed in bambara groundnut landraces may be due to decreases in chlorophyll especially in newly expanded leaves as a result of a general decrease in metabolic processes due to the decreased tissue water content. The production of reactive oxygen species (ROS) is also associated with chlorophyll destruction under drought conditions (Alaei, 2011). It is known that, water deficit increases the activity of chlorohpyllase, an enzyme responsible for breakdown of chlorophyll, which results in a decrease in the amount of chlorophyll (Alaei 2011; Muhammad and Massawe, 2015). According to Arunyanark et al. (2008) water deficit stress has been known to negatively affect chlorophyll content in many crops hence reducing photosynthetic ability.

In this study, the resistant bambara landrace S19-3 showed higher chlorophyll content values vs DodR and NALBAM 4 at both flowering and pod development stages indicating its ability to withstand water deficit stress. This trait can be considered to be a line of defence against drought which can result in drought resistance (Vurayai et al., 2011a). Interestingly, and contrary to bambara groundnut landraces, groundnut (MNANJE) showed increased chlorophyll content index (CCI) under water deficit stress. Painawadee et al. (2009) and Koolachart et al. (2013) have reported similar results. Mamadou et al. (2016), reported groundnut genotypes with high values of CCI under water stress to be drought stress resistant. High levels of CCI and the increase in CCI in groundnut under water deficit conditions is

associated with its ability to maintain its relative leaf water content, increase thickness of the leaves and chlorophyll density (increased darker green colour) at early stages of the drought condition (Songri et al., 2009; Mamadou et al., 2016). Maintaining chlorophyll concentration under water deficit stress was suggested as a drought resistance mechanism in many crop plants (van der Mescht et al., 1999) and in groundnut (Sheshshayee et al., 2006; Boontang et al., 2010; Savita et al., 2014).

The CCI is an indicator of the photo-synthetically active light-transmittance characteristics of the leaf (Richardson et al., 2002). It has been suggested that, CCI can be used as a criterion for selection of groundnut genotypes for drought resistance (Arunyanark et al., 2008). The maintenance of higher chlorophyll content in MNANJE as compared to bambara groundnut could be related to its ability to accumulate higher levels of proline during drought periods. Proline acts as a buffer against ROS damages (Vendruscolo et al., 2007), and hence could have protected the destruction of chlorophyll in MNANJE (the groundnut).

Relative water content (RWC) (%)

Water stress during flowering (25 – 49 DAE) and pod development (49 – 76 DAE) stages of growth of bambara groundnut and groundnut decreased RWC. Effects of decreased RWC include stomatal closure (Gindaba et al., 2004) and decreased CO_2 assimilation (Li et al., 2011). The reduction in RWC observed in this study could be associated with the decrease observed in gas exchange parameters. Water deficit in plants occurs when water loss due to the transpiration exceeds water absorption by roots (Berkowitz, 1998) and hence reduced RWC. Subsequently, plants tend to reduce water loss by reducing transpiration rate (stomatal closure). This results in a decrease in both stomatal conductance and CO_2 intake (Davies and Zhang, 1991; Davies et al., 1994). Plants stressed during pod development showed the lowest

percent change in RWC as compared to plants stressed during flower development. This may be because the plants were on their last stage of growth hence there was a decrease in metabolic activities (Yordanov et al., 2003; Farooq et al., 2009) compared to those at the flowering growth stage. The significant differences in relative leaf water content (RWC) observed in water stressed and non-stressed plots in this research, is evidence of the negative effect of water stress. These results are consistence with the results of Madhusudhan et al. (2002); Vurayai et al. (2011a); Ranganayakulu et al. (2015) who observed significant reduction of leaf RWC in stressed leaves of bambara groundnut and groundnut plants than in control plants.

The differences existed in RWC among the bambara groundnut landraces suggests the degree of drought resistance among the landraces (Schonfeld et al., 1988). RWC is an important trait, which indicates drought resistance as species which exhibit restricted changes in RWC per unit reduction of water potential are often considered to be relatively drought resistant. In the present study, there was a progressive reduction in leaf RWC in both species during water stress. The resistant bambara groundnut landrace S19-3, maintained relatively higher leaf RWC than DodR and NALBAM 4. However, MNANJE, the groundnut, found to maintain both higher levels of relative water content and lower percent decrease values than S19-3.

Yield and yield components

The reduced yield components observed in the bambara groundnut and groundnut landraces resulted in decreased final grain yield in the water deficit stressed plants. This indicates that, final yield depends very much on the performance of individual or combined yield components. Water deficit stress decreased final grain yield as a consequence of reduced pods per plant, seed number and 100 seed weight. Similar results have been reported by

Berchie et al. (2012); Mabhaudhi et al. (2013); Abejide et al. (2018) in bambara groundnut and Ratnakumar and Vadez (2011); Vaidya et al. (2015) in groundnut. Regardless of time of imposition of water deficit stress, both species produced yields under limited water conditions, although lower than in controls. This proves that these two crop species can survive and give yields under drought conditions; bambara groundnut (Linnemann and Azam-Ali, 1993; Ntundu et al., 2006) and groundnut (Vorasoot et al., 2003; Painawadee et al., 2009; de Lima Pereira et al., 2016).

The significant differences in yields and percentage changes, between control and stressed plants, observed in bambara groundnut landraces indicates that genetic variation exists among them. Soil water deficit stress also decreased grain yield of the groundnut (MNANJE). In both species, higher yield loss was found in plants that were water deficit stressed during flowering than plants stressed during pod development. In this study, the higher yield losses observed in plants stressed during flowering is associated with poor flower bud initiation (Bita and Gerats, 2013; Bishop et al., 2016), flower deformation and abortion. The reduction in yield observed in plants under water deficit stress during pod development were associated with shortened pod development period (Singh, 2011), insufficient soil moisture in the pod zone (Boote and Ketring 1990) and poor filling of the embryos which resulted to decreased 100 seed weight and shelling percentage (Vorasoot et al., 2003). Decreased 100 seed weight and shelling percentage, subsequently reduced final total grain yield.

As opposed to other yield components, 100 seed weight and shelling percentage showed higher percentage decrease during pod development as compared to flowering stage (*Table 5.3.4*). This is related with poor filling of seeds as during pod development stage involves seed formation, growth and development; while in flowering stage seed formation has yet to start.

5.5 Conclusion

The results obtained in this study showed differences existed among bambara groundnut landraces as well as between the two species in response to water deficit stress. The degree of drought resistance depends on the interactions between the landraces, drought intensity and the stage of plant growth. Drought occurring during flowering is more harmful than the one occurring during pod development. In the current study, it was noted that, stomata are the main driver of most of physiological processes under either water deficit conditions or normal supply of water. The reduction in the gas exchange parameters, as caused by stomatal closure, for preservation of water in plants indirectly affected the economic yield of the plants. Among the parameters studied, RWC, stomatal conductance, leaf proline content and chlorophyll content are important traits for selecting drought resistant plant species and or genotypes. Plants that accumulate high proline content maintain metabolic activities (e.g. photosynthesis) even under water deficit stress because of their ability to control osmotic adjustments. The results indicated that the negative effects of drought was more in bambara groundnut landraces than in groundnut. S19-3 was identified as drought resistant withstanding drought stress than DodR and NALBAM 4, but inferior to MNANJE (groundnut).

Decrease in stomatal conductance, transpiration, photosynthesis and increase in proline content points to the possibility of a drought avoidance strategy. In addition, proline accumulation could be associated more with drought tolerance mechanisms rather than drought avoidance; this is because when proline acts as scavenger against ROS or osmoprotectant against heat caused by water deficit, stomata do not necessarily close. Earliness to maturity shows the ability of plants to complete their life cycle before interruption of insufficient water supply, and hence is a drought escape mechanism. Increase in chlorophyll

content in MNANJE is a unique response for groundnut in mitigating drought conditions and it may be related to drought tolerance mechanism. It was also found that, the studied species mitigate water deficit conditions via more than one drought resistance mechanism. Drought escape, avoidance and tolerance were all shown by MNANJE and S19-3 although varied in their response. NALBAM 4 and DodR utilized only drought avoidance mechanism.

CHAPTER SIX

Influence Of Water-Deficit Stress On Morphological and Root Traits of Bambara Groundnut (*Vigna Subterranea* (L.) Verdc) and Groundnut (*Arachis Hypogaea* L.) Grown in Phenyl Vinyl Chloride (Pvc) Columns

6.1 Introduction

Water-deficit has negative effects on agriculture (Sazares et al*.,* 2011). The changes in the availability and distribution of rainfall because of fluctuations in climate have been reported to be more pronounced than in early 19th century (James, 1990; Araus et al., 2002; Rowhani et al., 2011; Thompson et al., 2015). With respect to farming community (farmers) agricultural drought is of the greatest concern. With the potential risk of increased frequency and intensity of water scarcity allied with climatic variations (Hassan, 2006); soil water limited resistant crops are expected to play a vital role in agricultural activities (Berchie et al., 2012). Neglected and ignored crop species have been informed to probably evolve to be drought resistant because of continuous cultivation in poor resource environments. Bambara groundnut (*Vigna subterranea* (L.) Verdc) is one of those drought resistant crops (Collinson et al., 1997; Al Shareef et al., 2013; Mabhaudhi et al., 2013). However, due to variability that exists among bambara groundnut landraces (Massawe et al., 2005), it is important to assess bambara landraces for drought resistance. One key step to achieving this is by understanding the mechanisms and plant adaptations to drought. Various reports show that, bambara groundnut is probably superior to most of grain legumes in terms of drought resistance (Massawe et al., 2005; Ibraheem et al., 2014; Muhammad, 2014). The crop is also resistant to high temperatures and survives on poor marginal soils where most other crops cannot (Linnemann and Azam-Ali, 1993; Muhammad, 2014). Furthermore, the crop is less susceptible

to pests and diseases than other crops, and can be cultivated with minimal amount of chemical or biological control (Linnemann and Azam-Ali, 1993; Tweneboah, 2000; Adzawla et al., 2015).

Root investigation is of importance as above ground plant studies, since the extraction of soil water and minerals is largely influenced by root system (Zhu et al., 2011). Therefore, studying roots is important for crop breeding (Fenta et al., 2014) in combating the current and future expected adverse effects of climate change. Roots are important in crop plants, they enable plants to respond, adapt and thrive in different environments (Paez-Garcia et al., 2015). Below ground parts of plants are more associated with drought resistance relative to shoot parts (Manavalan et al., 2010) and are the main contributor to crop yield (Narayanan et al., 2014) under water scarce conditions (Gupta et al., 2012). Several important root parameters like root length, root weight, root volume, root to shoot ratio, specific root length, branching pattern and horizontal distribution (Benjamin and Nielsen, 2004, 2006; Pace et al., 2010; Amoroso et al., 2010) have been measured and used to predict root functions within and among species. However, more investigation is necessary to further the understanding of many of the linkages between root forms and functions (Iverson, 2014).

Bambara groundnut being an under researched crop, very few studies have been done regarding its roots response to drought. On the other hand, many studies on drought resistance in groundnut (*Arachis hypogaea* L.) have been conducted worldwide; including its ability to extract water (Wright and Nageswara Rao, 1994; Benjamin and Nielsen, 2006; Taiz and Zeiger, 2006) and studies on root length density and rooting depth (Matsui and Singh, 2003). An experiment by Songsri et al. (2008) revealed that, groundnut genotypes with large root system and root depth are more favoured in dry areas. Junjittakarn et al. (2014) suggested root response under drought as an important mechanism to maintain high pod

yield, thus it can be considered as a criteria for selecting drought resistance in groundnut and so in other crops. Limited information is available on how bambara groundnut root systems respond to drought stress. Furthermore, limited information exist comparing root systems response to insufficient water supply for bambara groundnut and groundnut. Breeding for drought resistance can increase long term productivity under drought conditions. The present study therefore aimed at characterizing roots in bambara groundnut and groundnut landraces under water deficit and well-watered conditions. This information is helpful in developing future strategies to improve bambara groundnut and groundnut breeding for water deficit environments.

6.2 Materials and Methods

6.2.1 Experimental site

The experiment was conducted in a rainout shelter at the University of Nottingham Malaysia (2.946751°N, 101.8738529°E, 59 masl) in two consecutive years (2017 and 2018). Soil characterization for physical and chemical properties was done for both years. Soil textural class was loamy sand (section 6.3.1). The environmental conditions recorded during the trial periods (2017 and 2018) included photosynthetically active radiation (PAR), maximum and minimum daily temperatures and relative humidity (*Figure 5.3.1*).

6.2.2 Measurements of root parameters

The first destructive sampling and measurements was done at 25 days after emergence. Other sets of data were taken at the end of the first drought period (49 DAE), which coincided with the start of the second water stress period. The last two data sets were taken at the end of the second water deficit period (76 DAE) and at harvesting (ranging 90 – 112 DAE). Roots were

carefully extracted from the phenyl vinyl chloride (PVC) columns by opening the columns followed by gentle application of tap water to remove the soil. Roots were then placed inside a tray filled with water for further removal of the remaining soil particles and other debris. The rooting depth was taken immediately and the roots including broken root parts were packaged in poly paper bags and kept in refrigeration before scanning with subsequent determination of root dry weights. The following root traits were obtained from winRhizo analysis; root length (RL), surface area (SA), average diameter (AD) and average volume (AV). Scanning of the roots was done by Epson Perfection 4990 Photo (Epson America, Long Beach, California, USA) using the WinRhizo (Regent Instruments, Quebec, Canada) programme. The roots were floated in water in acrylic trays on the scanner. The scanning resolution of 400 dpi in 20 x 30 cm trays was used (Bouma et al., 2000).

6.3 Results

6.3.1 Soil physical and chemical characteristics

Soil physical and chemical characteristics were determined. The soil properties are presented in Chapter 5, in section 5.3.2 (*Table 5.3.1).*

6.3.2 Weather conditions

Weather data for the two cropping seasons, 2017 and 2018, at the University of Nottingham Malaysia rain out shelter are available in Chapter 5 section 5.3.2 (*Figure 5.3.1).*

6.3.3 Combined Analysis of Variance (ANOVA)

Following separate analysis of variance, results revealed existence of significant ($p < 0.05$) differences between the landraces, water regimes and their interactions. Test for homogeneity of variances between two years showed no significant ($p > 0.05$) differences,

hence combined analysis of variance was performed. The results for the combined analysis are presented in *Appendix 3, Appendix 4 and Appendix 5*. The interactions between years and water regimes were only significant ($p < 0.05$) for average root diameter during flowering (*Appendix 4*) and total root length during pod development (*Appendix 5*). Interactions between landraces and years were significant for average root diameter (*Appendix 4*), total root length and root volume (*Appendix 5*). The interactions between years, water regimes and landraces were significant ($p < 0.05$) for canopy spread and root to shoot ratio during pod development only (*Appendix 3*). Also interactions between years, water regimes and landraces were significant ($p < 0.05$) for total root length and root volume (*Appendix 5*).

6.3.4 Soil moisture content

Landraces under varying soil moisture content

The growth and development of plants differed significantly ($p < 0.001$) between the well-irrigated plants (controls) and the plants that were subjected to water deficit stress during flowering and pod development. Also significant ($p < 0.001$) differences were observed between the landraces. Although analysis of variance was done separately for bambara groundnut landraces and groundnut, differences in water consumption between the two species were clear (*Figure 6.3.1* and *Figure* 6.3.2). Among the bambara groundnut landraces, S19-3 was found to consume more available soil moisture followed by DodR and NALBAM 4. On the other hand, water consumption by MNANJE (groundnut) was higher than that of S19-3 *(Figure 6.3.1* and *Figure* 6.3.2). Significant ($p < 0.001$) differences among interactions of landraces and water regimes also existed *(Figure* 6.3.1 and *Figure* 6.3.2). In all cases, MNANJE was superior in extracting soil moisture content in all water regimes followed by S19-3, DodR

and NALBAM 4. This is evidenced with the amount of soil moisture remained in the soil during measurement (*Figure 6.3.1* and *Figure* 6.3.2).

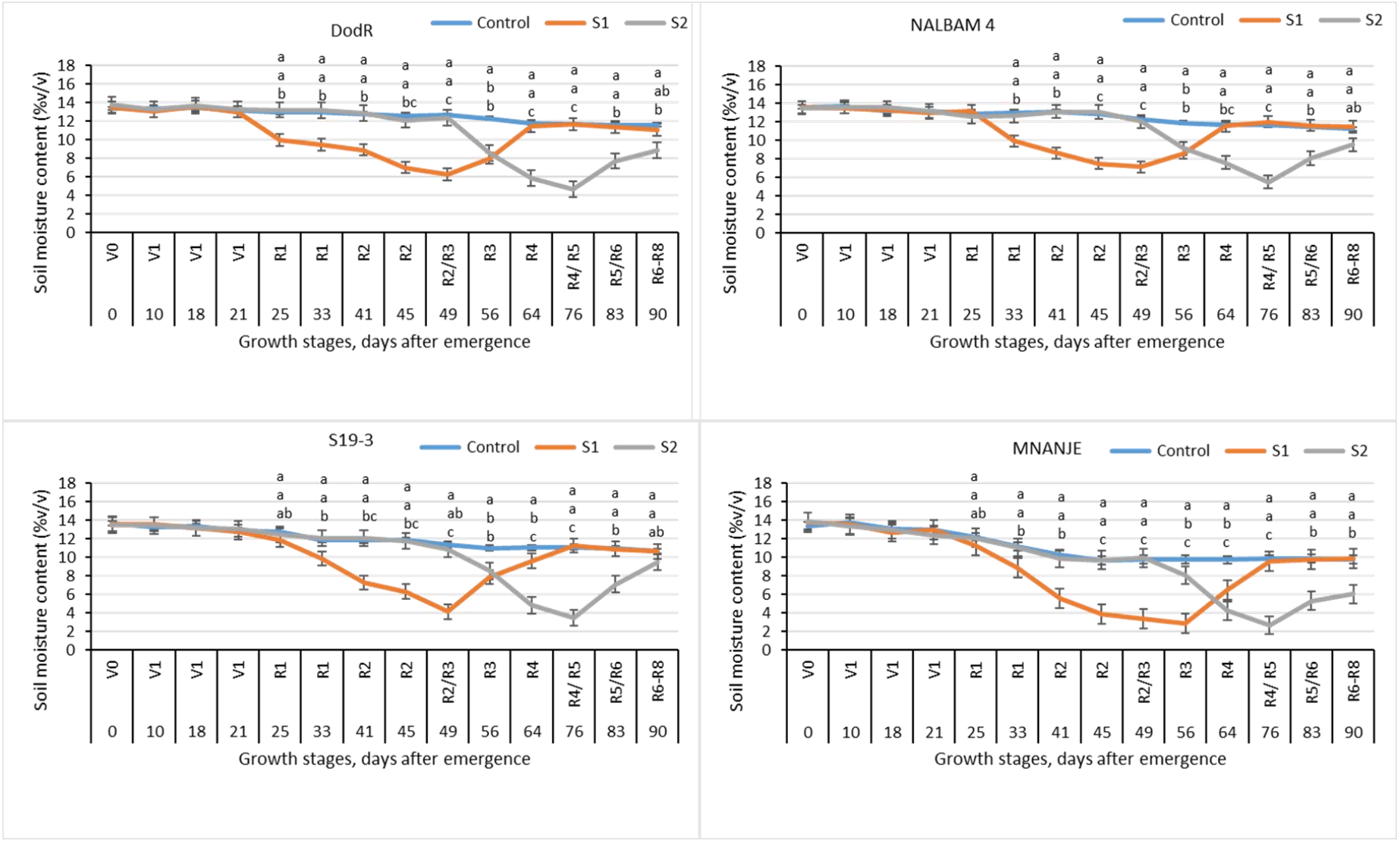


Figure 6.3.1: Variations in soil moisture extraction by different bambara groundnut (DodR, NALBAM 4, S19-3) and groundnut (MNANJE) landraces under varying water regimes. V1 = Vegetative, R1 = Flowering, R2 = Beginning peg, R3 =Beginning pod, R4 = Full pod, R5 = Beginning seed, S1 = water stress during flowering, S2 = water deficit stress during pod development. (n = 6).

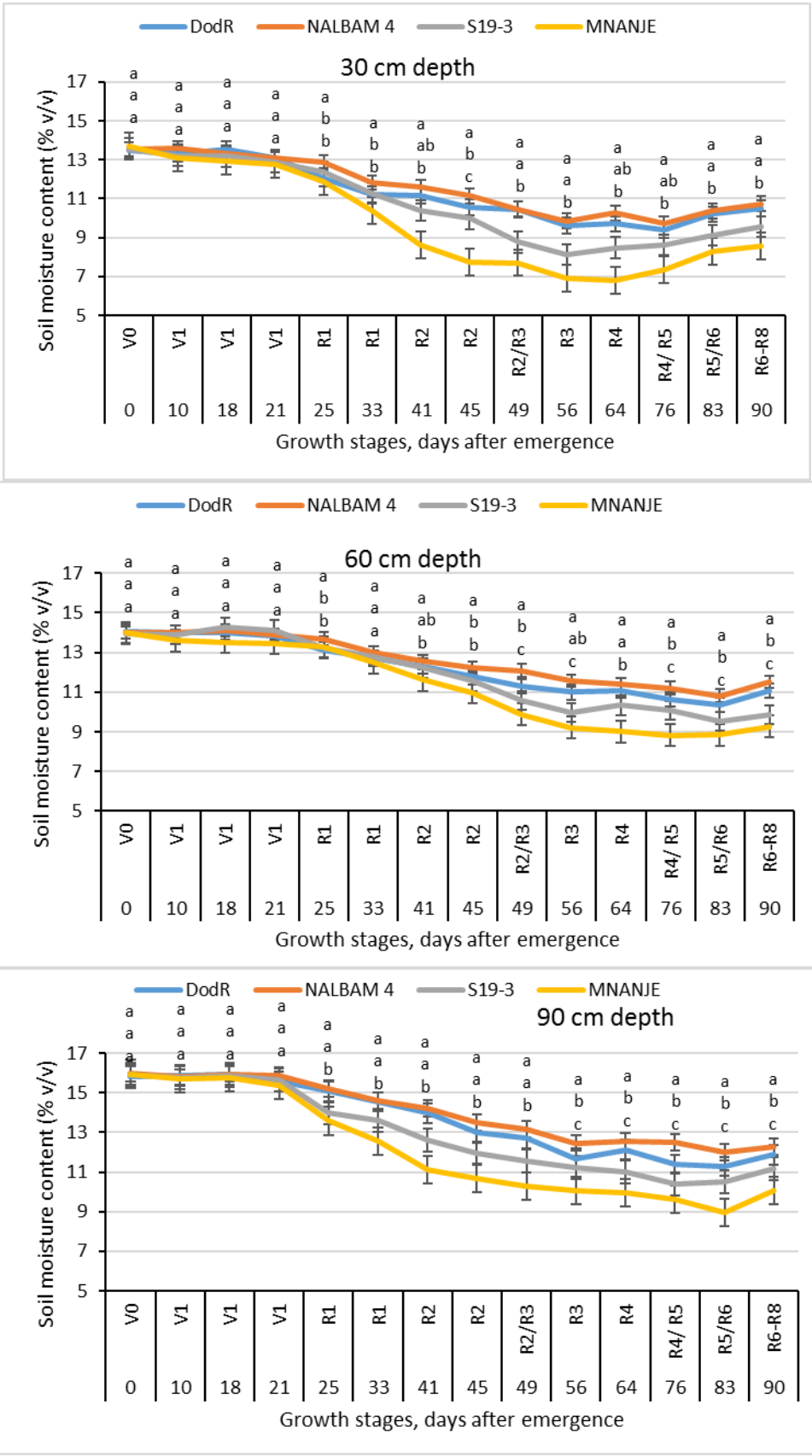


Figure 6.3.2:Combined variations in soil moisture content in different bambara groundnut (DodR, NALBAM 4, S19-3) and groundnut (MNANJE) landraces at different soil depths (30 cm, 60 cm and 90 cm) during 2017 and 2018 cropping seasons in rain out shelter experiment at University of Nottingham Malaysia. V = vegetative, R1 = Beginning of bloom, R2 = Beginning peg, R3 =Beginning pod, R4 = Full pod, R5 = Beginning seed, R6 - R8 = Maturity. (n = 6).

6.3.5 Root traits

Rooting depth

Highly significant differences ($p < 0.001$) for rooting depth were found among the landraces, among the water regimes and the interaction between landraces and water regimes (*Table 6.3.1)*. Neither interaction between landrace and years nor water regimes and years gave significant ($p > 0.05$) differences. The only significant difference ($p = 0.04$) was observed in interaction between landraces, water regimes and years (*Appendix 4*) during flowering. The difference between water stressed and control plants was highest in plants stressed during flowering. Among bambara groundnut landraces, S19-3 showed the longest rooting depth followed by DodR and NALBAM 4 (*Table 6.3.1*). In addition, S19-3 had the lowest percentage rooting depth changes followed by DodR and lastly NALBAM 4. MNANJE, the groundnut, had the longest roots as compared to bambara groundnut landraces. In most cases, MNANJE experienced the lower percent changes in rooting depths between control and water stressed plants. The decrease in rooting depth between control and stressed plants during flowering and pod development were NALBAM 4 (26% and 3%), DodR (18% and 8%) and S19-3 (15% and 6%), respectively. The decrease in rooting depth in MNANJE were 13% and 5% for plants stressed during flowering and pod development respectively.

Root length density (RLD)

Water deficit significantly ($p < 0.001$) increased the root length density (*Table 6.3.1*). Highly significant differences ($p < 0.001$) existed among landraces and in interaction between landraces and water regimes. Significant differences ($p < 0.05$) were also found in the interaction between landraces and years. The interaction between landraces, water regimes and years showed significant ($p = 0.012$ and $p = 0.024$) differences during flowering and pod

development, respectively (*Appendix 5*). At the end of flowering stress, stressed plots were found to have higher RLD (477 cm^{-2}) as compared to control (371 cm^{-2}) plots, with a percentage increase of 29%. The same trend was experienced during pod development stress with smaller values of RLD and higher percentage increases (*Table 6.3.1*). In both water stress periods, S19-3 was found to be superior among the bambara groundnut landraces. In addition, the lowest changes among bambara groundnut landraces was shown by S19-3. MNANJE, on the other hand, had the lowest RLD values during flowering and pod development stress periods. MNANJE also showed the smallest percentage change at the end of pod development stress compared to bambara groundnut landraces, but had higher percentage increase during flowering stress in comparison with S19-3 which had the lowest among the other bambara groundnut landraces.

Total root length

The results for the total root length are presented in *Table 6.3.1*. Highly significant ($p < 0.001$) differences in total root length were observed among the water regimes. A highly significant difference ($p < 0.001$) was also found in the interaction between landraces and water regimes. The interactions between landraces and years; and between water regimes and years gave significant differences at ($p < 0.001$) during pod development (*Table 6.3.1*, *Appendix 5*). A highly significant difference ($p < 0.001$) existed in the interaction between landraces, water regimes and years (*Appendix 3*). Control plots had higher values of total root length as compared to water deficit stressed plots during flowering and pod development. In this study, plants that were water stressed during flowering had the highest percentage changes relative to control. Among bambara groundnut landraces, S19-3 had the longest total root length, with the lowest percentage changes between control and water stressed plots, followed by DodR (*Table 6.3.1*). On the other hand, MNANJE outperformed all bambara groundnut landraces

both in control and stressed plants. The decrease in total root length between control and water stressed plots were lowest in MNANJE during both flowering and pod development water deficit stress periods.

Root volume

Significant ($p < 0.001$) differences were observed between water regimes (WR) and among bambara groundnut landraces (L) (*Table 6.3.1*). Significant differences ($p < 0.001$) were also observed in the interaction between L and WR; and between L and years (Y). The interaction between L, WR and Y was significant ($p < 0.05$) only during flowering (*Appendix 5*). Regardless of separate analyses done, clear differences in root volume existed between bambara groundnut landraces and groundnut (*Table 6.3.1*). At the end of water deficit stress during pod development, S19-3 had the highest root volume (37 cm^3) followed by DodR (32 cm^3) and NALBAM (29 cm^3). The percent change in root volume between control plots and water stressed plots was 43% for both flowering and pod development stress periods (*Table 6.3.1*). During flowering stress, the lowest percentage reduction was 34% in S19-3, while for DodR and NALBAM 4 percentage decrease were 54% and 58% respectively. Similar trends were observed at the end of pod development stress, whereby percentage changes were 49%, 55% and 60% for S19-3, DodR and NALBAM 4 respectively. Highest root volume values and lowest percentage change for root volume were observed in MNANJE, the groundnut, throughout the experiments. At the end of pod development stress, MNANJE had on average a root volume of 41 cm^3. Root volume percentage decrease (from control) in MNANJE were 27% and 24% during flowering and pod development stress periods respectively.

Table 6.3.1: Mean changes in rooting depth (cm), total root length (cm), root volume (cm^3) and root length density (cm^{-2}) in bambara groundnut and groundnut (MNANJE) landraces during growth stages as affected by water deficit stress in two consecutive cropping seasons (2017 and 2018).

		Rooting depth (cm)				Total root length (cm)				Root volume (cm^3)				Root length density ($cm.cm^{-3}$)			
Treatments		S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ
Water regimes	Control	94.98[a]		110.30[a]		2635.00[a]		4239.00[a]		7.43[a]		32.40[a]		371.00[b]		130.70[b]	
	Stressed	78.44[b]	-17	103.70[b]	-6	1789.00[b]	-32	3316.00[b]	-22	4.24[b]	-43	18.33[c]	-43	477.70[a]	29	192.70[a]	47
Landraces	DodR	86.17[b]		99.40[b]		2193.00[b]		3542.00[b]		4.74[b]		22.70[b]		493.30a		168.20[a]	
	NALBAM 4	76.95[c]		94.50[c]		1674.00[c]		3264.00[c]		4.14[c]		22.99[b]		417.70[b]		150.10[b]	
	S19-3	104.07[a]		119.70[a]		3177.00[a]		4114.00[a]		10.02[a]		27.53[a]		319.30[c]		157.20[ab]	
	MNANJE	112.7		123.8		3551.67		4482.33		13.78		37.14		323.2		125.00	
Interaction																	
Control	DodR	92.13[c]		107.50[c]		2495.00[c]		4054.00[b]		5.97[c]		32.03[b]		418.50[c]		126.70[c]	
Control	NALBAM 4	85.08[d]		98.60[d]		1930.00[d]		3601.00[c]		4.98[d]		29.78[c]		387.40[cd]		129.70[c]	
Control	S19-3	112.73[a]		124.80a		3481.00[a]		5061.00[a]		11.34[a]		37.39[a]		307.20[f]		135.50[bc]	
Stressed	DodR	75.22[e]	-18	98.40[d]	-8	1591.00[e]	-36	3132.00[f]	-23	2.73[e]	-54	14.30[e]	-55	602.90[a]	44	219.50[a]	73
Stressed	NALBAM 4	62.88[f]	-26	89.40[de]	-9	1204.00[f]	-38	2792.00[g]	-22	2.11[e]	-58	11.80[d]	-60	484.80[b]	25	236.32[bc]	82
Stressed	S19-3	96.22[b]	-15	117.30[b]	-6	2572.00[b]	-26	4025.00[b]	-20	7.50[b]	-34	18.89[d]	-49	345.40[e]	12	213.90[a]	58
Water regime	p ≤ 0.05	<.001		<.001		<.001		<.001		<.001		<.001		<.001		0.003	
Landrace	p ≤ 0.05	<.001		<.001		<.001		<.001		<.001		<.001		<.001		0.043	
Interaction	p ≤ 0.05	<.001		<.001		<.001		<.001		<.001		<.001		<.001		<.001	
Control	MNANJE	118[a]		128.2[a]		3682[a]		5344[a]		14.83[a]		46.64[a]		114.5798[b]		107.7[b]	
Stressed	MNANJE	103.1[b]	-13	121.5[b]	-5	3301[b]	-10	4678[b]	-12	10.79[b]	-27	35.56[c]	-24	131.5523[a]	15	164.00[a]	52
	p ≤ 0.05	<.001		<.001		<.001		<.001		<.001		<.001		<.001		<.001	

Values followed by the same superscript are not significantly different according to Duncan's Multiple Range Test (DMRT). % Δ = percentage change between control and water stressed plants, S1 = water deficit stress during flowering, S2 = water deficit stress during pod development. Groundnut (MNANJE) landrace was used for comparison. Analysis of variance was done separately for each species. (n = 6).

Average root diameter

The results of the impact of insufficient water application on average root thickness are shown in *Table 6.3.2*. Insufficient water supply significantly ($p < 0.001$) increased the average root diameter in water stressed plots as compared to control plots. Bambara groundnut landraces differed significantly ($p < 0.001$) during the experiments. The interaction among landraces and water treatments differed significantly at ($p < 0.001$) during flowering and at ($p = 0.018$) during pod development. The interactions between landraces and years; and among water treatments and years varied significantly at ($p < 0.05$). The interaction between landraces, water regimes and years did not show any significant ($p > 0.05$) difference (*Appendix 4*). Higher percentage increase (over control plots) values were observed in plots that were water stressed during pod development as compared to plants which were water deficit stressed during flowering. Among bambara groundnut landraces, S19-3 had the thickest average root diameter under all water treatments. The highest values of average root diameter were shown by MNANJE throughout. The highest percentage increase in average root diameter during flowering stress was observed in S19-3 (37%) and the lowest percent increase was observed in MNANJE (19%). At the end of water stress during pod development, NALBAM 4 (34%) showed the highest percentage increase and the lowest percentage increase was found in DodR (18%).

Root surface area

Root surface area showed significant ($p < 0.001$) variations among water treatments and among bambara groundnut landraces (*Table 6.3.2*). The interaction between water regimes and landraces was also significant ($p < 0.001$). However, no significant variations ($p > 0.05$) found in the interactions between landraces and years; water regimes and years or interaction

between landraces, water regimes and years (*Appendix 4*). The percentage reduction in root surface area due to water deficit stress did not differ significantly between flowering stress (19%) and pod development stress (20%) as compared with control plots (*Table 6.3.2*). S19-3 showed the highest root surface area among the bambara groundnut landraces. At the end of water deficit stress during flowering, S19-3 had a root surface area of 1108 cm^2 followed by DodR (831 cm^2) and the lastly NALBAM 4 (811 cm^2). The highest percent change among the bambara groundnut landraces during flowering stress was observed in NALBAM 4 (23%) and the lowest in S19-3 (17%). At the end of stress during pod development, the highest percent decrease was found in DodR (21%) and the lowest in S19-3 (19%). MNANJE, (the groundnut), had highest root surface area values in both well-irrigated as well as in droughted treatments. MNANJE showed the highest percent decrease in root surface area during pod development stress (23%) while during flowering stress the decrease was by 21% from the control. This change is higher than the percentage changes expressed by S19-3 (17%) and DodR (20%) during the same water stress periods.

Table 6.3.2: Mean changes in root surface area (cm^2) and average root diameter (mm) in bambara groundnut and groundnut (MNANJE) landraces during growth stages as affected by water deficit stress in two consecutive cropping seasons (2017 and 2018).

		Surface area (cm^2)				Average root diameter (mm)			
Treatments		S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ
Water regimes	Control	444.00^{a}		1025.30^{a}		0.52^{b}		0.76^{b}	
	Stressed	358.50^{c}	-19	820.40^{c}	-20	0.65^{a}	26	0.96^{a}	27
Landraces	DodR	328.20^{c}		831.10^{b}		0.53^{c}		0.68^{c}	
	NALBAM 4	334.90^{b}		811.20^{c}		0.56^{b}		0.80^{b}	
	S19-3	560.40^{a}		1108.20^{a}		0.60^{a}		1.07^{a}	
	MNANJE	655.43		1200.67		0.67		1.34	
Interaction									
Control	DodR	377.10^{c}		955.40^{c}		0.49d		0.63^{f}	
Control	NALBAM 4	362.90^{d}		898.90^{d}		0.52^{cd}		0.67^{ef}	
Control	S19-3	592.00^{a}		1221.60^{a}		0.53^{c}		0.97^{bc}	
Stressed	DodR	301.20^{e}	-20	755.50^{fd}	-21	0.60^{b}	21	0.74^{def}	18
Stressed	NALBAM 4	280.30^{f}	-23	715.20^{g}	-20	0.63^{b}	21	0.90^{bcd}	34
Stressed	S19-3	493.90^{b}	-17	990.60^{c}	-19	0.73^{a}	37	1.2^{4a}	28
Water regime	p < 0.05	<.001		<.001		<.001		0.006	
Landrace	P < 0.05	<.001		<.001		<.001		<.001	
Interaction	p < 0.05	<.001		<.001		<.001		0.018	
Control	MNANJE	705.4^{a}		1347^{a}		0.629^{b}		1.208^{b}	
Stressed		556.8^{b}	-21	1032^{c}	-23	0.7465^{a}	19	1.535^{a}	27
	p ≤ 0.05	<.001		<.001		<.001		0.002	

Values followed by the same superscript are not significantly different according to Duncan's Multiple Range Test (DMRT). % Δ = percentage change between control and water stressed plants, S1 = water deficit stress during flowering, S2 = water stress deficit during pod development. Groundnut (MNANJE) landrace was mainly used for comparison. Analysis of variance was done separately for each species. (n = 6).

6.3.6 Morphological traits

Plant height and canopy spread

Results of plant height and canopy spread (*Table 6.3.3*) during the experiments significantly ($p < 0.05$) differed among water treatments and landraces. The interactions among landraces and water treatments for height was significant at ($p < 0.05$) while that of canopy spread was significant at ($p < 0.001$) (*Table 6.3.3*).The interactions with regard to effect of years showed that, only interaction between landraces, water treatments and years was significant ($p < 0.05$) in canopy spread (*Appendix 3*). None of the interactions showed any significant ($p > 0.05$) effect on plant height. The DodR landrace had the highest values of plant height and canopy spread, followed by NALBAM 4 and lastly S19-3. There was a consistent trend of decreasing plant height and canopy spread in response to water deficit stress. The highest percentage change in both plant height and canopy spread were observed in water deficit stress during

flowering. The DodR landrace showed the greatest percentage decrease in plant canopy spread and height under both water deficit stress periods relative to NALBAM 4 and S19-3. With respect to MNANJE, the groundnut, significant ($p < 0.001$) variations existed among water treatments at both flowering and podding stages. Plants that were water deficit stressed during flowering were more affected relative to plants stressed during podding. MNANJE had the highest values for plant height (52.94 cm) and canopy spread (71.30 cm) as compared to individual bambara groundnut landraces. In addition, MNANJE revealed the highest percentage decrease values in both flowering and pod development water deficit stress periods.

Table 6.3.3: Combined plant height and canopy spread of bambara groundnut (DodR, NALBAM 4 and S19-3) and groundnut (MNANJE) grown under well irrigated and water deficit conditions during 2017 and 2018 seasons.

		Plant height (cm)				Canopy spread (cm)			
		S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ
Water regimes	Control	28.00^{a}		32.06^{a}		42.62^{a}		60.79^{a}	
	Stressed	25.84^{a}	-8	30.18^{b}	-6	33.58^{b}	-21	50.77^{b}	-16
Landraces	DodR	27.89^{b}		30.93^{b}		40.28a		53.42^{a}	
	NALBAM 4	30.10^{a}		32.75^{a}		40.37^{a}		52.83^{a}	
	S19-3	25.01^{c}		29.42^{c}		37.54^{d}		50.91^{b}	
	MNANJE	36.74		52.94		51.84		71.3	
Interaction									
DodR	Control	29.64^{abc}		32.53^{ab}		43.93^{bc}		66.18^{a}	
	Stressed	26.97^{cd}	-9	30.33^{bc}	-7	33.67^{e}	-23	52.34^{de}	-21
NALBAM 4	Control	31.10^{ab}		33.30^{a}		42.65^{abc}		55^{c}	
	Stressed	29.60^{ab}	-5	32.37^{ab}	-3	34.3^{d}	-20	46.87^{e}	-15
S19-3	Control	25.58^{de}		30.33^{bc}		41.27^{bc}		58.2^{b}	
	Stressed	24.67^{e}	-4	29.45^{c}	-3	33.78^{e}	-18	51.12^{e}	-12
Water regimes	p-value	0.036		0.024		<.001		<.001	
Landraces	p-value	<.001		<.001		<.001		0.004	
Interaction	p-value	0.03		0.083		<.001		<.001	
MNANJE	Control	39.46^{a}		56.73^{a}		56.48^{a}		76.27^{a}	
	Stressed	31.97^{b}	-19	49.1^{b}	-13	42.72^{c}	-24	65.17^{c}	-15
	p-value	0.001		<.001		<.001		<.001	

Values followed by the same superscript are not significantly different according to Duncan's Multiple Range Test (DMRT). % Δ = percentage change between control and water stressed plants, S1 = water deficit stress during flowering, S2 = water stress deficit during pod development. Groundnut (MNANJE) landrace was used for comparison. Analysis of variance was done separately for each species. (n = 12).

Shoot dry weight, root dry weight and root to shoot dry weight ratio

Table 6.3.4 shows data for shoot dry weight, root dry weight and root to shoot dry weight ratio. Drought at different phenological stages of bambara groundnut and groundnut

significantly ($p < 0.001$) reduced shoot dry weight and root dry weight as compared to control plants. Similarly, landraces significantly differed ($p < 0.001$) in shoot dry weight and root dry weight. The interaction between landraces and water regimes for shoot dry weight was significant ($p < 0.001$) during both flowering and pod development. For root dry weight, the interaction between landraces and water regimes was significant ($p < 0.001$) during flowering and at ($p = 0.001$) during podding stage (*Table 6.3.4*).

Among the bambara groundnut landraces, DodR had the highest values of dry shoot weight, while the lowest values were found in S19-3. Highest percentage decrease was found in NALBAM 4, while S19-3 showed the smallest percent decrease in both shoot dry weight and root dry weight (*Table 6.3.4*). Contrarily, MNANJE had the highest shoot dry weight in controls and in plants which were water deficit stressed. At the termination of flowering water limited stress, MNANJE showed the highest percent decrease, while at the termination of pod development water limited stress revealed the least percentage decrease in shoot biomass. Root biomass was more reduced during water deficit stress imposed at flowering as compared to pod development. Bambara groundnut landraces were more sensitive to drought during flowering stage relative to pod development stage. Among the bambara groundnut landraces, S19-3 gave the highest values of root mass throughout, whereas NALBAM 4 experienced lowest values of root dry weight throughout. Highest percentage changes were observed in DodR. MNANJE had the highest shoot and root dry weights as compared to individual bambara groundnut landraces. Lowest values in percentage change between stressed and control plants were found in MNANJE as compared with bambara groundnut landraces (*Table 6.3.4*).

Root to shoot weight ratio differed significantly ($p < 0.001$) due to differences in soil moisture application. Landraces differed significantly ($p < 0.001$) in root:shoot ratio (*Table 6.3.4*). Also significant ($p < 0.001$) differences existed in the interaction between landraces and water regimes. Neither the interaction between landraces and years nor the interaction among water treatments and years gave any substantial ($p > 0.05$) variations for root to shoot ratio. The interaction between landraces, water regimes and years showed significant difference at ($p = 0.024$). Highest percentage increase in values between control and water deficit stress were found during flowering. Among the bambara groundnut landraces, S19-3 recorded the highest percent increase in root to shoot ratio in both stress periods. MNANJE had the highest root to shoot ratio values compared to bambara groundnut landraces during both stress periods. However, MNANJE had the highest root to shoot ratio percentage increase during flowering and lowest percentage increase during pod development.

Table 6.3.4: Water deficit stress effects on dry shoot biomass per plant (g), dry root biomass per plant (g) and root shoot ratio of bambara groundnut (DodR, NALBAM 4 and S19-3) and groundnut (MNANJE) landraces during two consecutive seasons (2017 and 2018).

Treatments		Shoot dry weight (g)				Root dry weight (g)				Root/Shoot ratio			
		S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ	S1	% Δ	S2	% Δ
Water regimes	Control	8.018^{a}		34.06^{a}		1.13^{a}		2.93^{a}		0.14^{b}		0.09^{b}	
	Stressed	3.928^{b}	-51	24.7^{c}	-28	0.86^{b}	-24	2.61^{c}	-11	0.22^{a}	52	0.11^{a}	30
Landraces	DodR	7.273^{a}		31.86^{a}		0.95^{b}		2.46^{b}		0.13^{b}		0.08^{b}	
	NALBAM 4	6.916^{a}		30.78^{a}		0.87^{c}		2.37^{c}		0.13^{b}		0.08^{b}	
	S19-3	6.262^{b}		28.67^{b}		1.41^{a}		3.57^{a}		0.23^{a}		0.12^{a}	
	MNANJE	33.72		70.47		7.775		9.715		0.230		0.138	
Interaction													
DodR	Control	8.808^{a}		34.34^{a}		1.04^{c}		2.60^{c}		0.12^{d}		0.08^{f}	
	Stressed	4.304^{c}	-51	25.88^{b}	-25	0.63d^{e}	-39	2.20c^{d}	-15	0.15^{c}	25	0.09^{cd}	12
NALBAM 4	Control	7.772^{b}		34.24^{a}		0.84^{d}		2.57^{c}		0.11^{d}		0.07^{f}	
	Stressed	3.24^{d}	-58	22.91^{c}	-33	0.46^{e}	-46	2.12^{d}	-17	0.14^{bc}	30	0.09d^{e}	23
S19-3	Control	7.473^{b}		33.59^{a}		1.52^{a}		3.71^{a}		0.20^{b}		0.11^{c}	
	Stressed	4.24^{c}	-43	25.3^{b}	-25	1.19^{b}	-21	3.56^{ab}	-4	0.28^{a}	39	0.14^{b}	27
Water regimes	p-value	<.001		<.001		<.001		<.001		<.001		<.001	
Landraces	p-value	<.001		0.001		<.001		<.001		<.001		<.001	
Interaction	p-value	<.001		0.001		0.098		<.001		0.01		0.14	
MNANJE	Control	43.23^{a}		75.77^{a}		8.72^{a}		9.89^{a}		0.202^{b}		0.131^{b}	
	Stressed	24.2^{b}	-44	65.18^{b}	-14	6.82^{b}	-21	9.54^{a}	-3	0.282^{a}	40	0.146^{a}	12
	p-value	<.001		<.001		<.001		<.001		<.001		0.002	

Values followed by the same superscript are not significantly different according to Duncan's Multiple Range Test (DMRT). % Δ = percentage change between control and water stressed plants, S1 = water deficit stress during flowering, S2 = water stress deficit during pod development. Groundnut (MNANJE) landrace was mainly used for comparison. Analysis of variance was done separately for each species. (n = 6).

6.4 Discussion

Soil moisture content and landraces

The current findings suggest that high values of rooting depth, root length density and root dry matter contributed to superior water extraction capacity observed in MNANJE and S19-3 under water stress conditions. Hamidou et al. (2018) reported similar results in groundnut while Cattivelli et al. (2008) reported similar observations in various genus *Vigna* crops. The higher rate of depletion of water in the reservoir shown by MNANJE and S19-3 as compared to DodR and NALBAM 4 can also be explained by high transpiration rates shown by MNANJE and S19-3. Whereas the higher amount of soil moisture in the reservoir shown by DodR and NALBAM 4 can be explained by low transpiration as a result of stomatal closure to conserve water (Jacqueline et al., 2016). Zaman-Allah et al. (2011); Zhou et al. (2014) demonstrated that drought resistant groundnut genotypes had higher water extraction than sensitive genotypes under drought conditions, which is the case for MNANJE and S19-3. Suneet (2016) pointed out that, water extraction under drought stress contributes to dehydration avoidance strategy. Under water stress conditions, high water consumption and higher transpiration observed in MNANJE and S19-3 compared to DodR and NALBAM 4, suggests that MNANJE and S19-3 use drought avoidance strategy to mitigate drought.

Rooting depth and root length density

Root is a key parameter allied with soil water limited conditions. For plants to access soil water, plants increase their rooting ability as well as volume **(**Blum, 2011; Fenta et al., 2014). It is claimed that, the more the volume of soil reached under drought, the more the yields of crops (Asif and Kamran, 2011). Root length density and rooting depth are important components for enhanced deep soil water extraction (Asif and Kamran, 2011; Borrell et al., 2014).

Advantages of a deeper and rapid growing roots for water deficit resistance already highlighted in different crop species like chickpea (Varshney et al., 2011; Chen et al., 2012; Jaganathan et al., 2015), rice (Bernier et al., 2009; Uga et al., 2013), maize (Hund et al., 2011), wheat (Wasson et al., 2012), and soybean (Sadok and Sinclair, 2011).

In the present study, rooting depth was reduced under water-limited plants as compared to well-irrigated plants. The current results agree with findings by Bandyopadhyay (2014). In the present study, wide variations in rooting depths and RLD existed among bambara groundnut landraces during both water deficit periods. In addition, differences were observed between bambara groundnut landraces and groundnut (*Table 6.3.1*). These variations display genotypic response of rooting depths and root length density to drought; and largely depends on how certain plant materials develop roots under water deficit stress. Faster growing and deep rooted plant materials, like groundnut, have been advocated as beneficial in tropical environments (Wright and Nageswara Rao, 1994). The present study revealed the superiority of MNANJE, the peanut/groundnut, in sustaining appreciable leaf hydration in times of drought relative to bambara groundnut landraces. This is partly caused by root proliferation in the lower soil layers. Devries et al. (1989), reported similar results, where peanut outweighed pigeon pea as well as soybean root proliferation and plant water status maintenance. The differences observed among the plant species and within the bambara groundnut landraces in all stages of plants' growth, proves the genetic potential of the plant materials under the current study. Groundnut was superior over bambara groundnut whereas S19-3 outweighed DodR and NALBAM 4 in terms of deep rooting and root length density characteristics. This implies that MNANJE and S19-3 can extract water held in deeper horizons during drought periods and hence are capable of attaining reasonable yields.

Increased early vigour results in deeper and faster root growth, forming more adventitious roots in the upper soil layer and are correlated with increased crop productivity under drought conditions (Turner et al., 2001; Vadez et al., 2013). MNANJE showed early vigour in both shoot and root, whereas S19-3 showed only early vigour in roots. It has long been considered that, improved rooting depth enhances resistance to water deficit in plants (Kashiwagi et al., 2006). In water limited conditions, Fang et al. (2017) have shown that deeper rooting increased yield in wheat. The ability shown by MNANJE and S19-3 of early penetration to deeper soil layers and enhanced root length density under water deficit stress, implies that the two plant materials possess useful root traits for drought resistance. Rooting depth is an important trait in drought conditions and can be used in breeding programmes.

Total root length

Early and rapid root growth is primarily a function of both lateral root commencement and development, which basically includes number of lateral roots, root surface area, volume of roots and root length density (Ye et al., 2018). Rapid growing roots have high ability of absorbing soil water from dry environments. MNANJE was found to have proliferative and vigorous root growth in early growth stages. The total root length values recorded under water-limited treatments were lower than those recorded in the well-watered conditions.

Current observations agree with findings reported by Sikuku et al. (2012) who worked with rice and Belachew et al. (2018) who worked on faba bean. The decline in root length due to drought could have been caused by reduced expansion of cells as a result of insufficient water supply to growth hormones which later on leads to decreased cell turgor, cell size followed by retarded cell growth (Banon et al., 2006). Plants that were water deficit stressed during flowering showed a higher percentage decrease relative to controls compared to plants

stressed during pod development (*Table 6.3.1*). This indicates that the flowering stage has relatively extensive root growth compared to the pod development stage. In the present study, there were distinct differences in total root length among bambara groundnut landraces as well as among the two legumes on how they responded to water deficit. Among bambara groundnut landraces, S19-3 had higher total root lengths compared to DodR and NALBAM 4 during both water deficit treatments. S19-3 also recorded the lowest percentage reduction from the control during both water deficit stress stages, while NALBAM 4 had the highest reduction. This implies that S19-3 was able to maintain root growth under water deficit treatment and apparently, this characteristic contributed highly towards higher drought resistance where deeper and extensive root systems contributed positively to water uptake (Huang and Gao, 1999).

MNANJE, contrarily, showed more massive roots than the drought-resistant bambara landrace, S19-3, thus MNANJE might be a possible crop for drought avoidance and or tolerance by improved access to deeper soil water. In addition to that, MNANJE reacted to water limited conditions through improved rooting depth as compared to S19-3, which was superior to DodR and NALBAM 4.

Average root diameter and volume

Root traits influence the amount of water and nutrient absorption of available soil water and nutrients. Roots play a role in maintenance of crop yield under drought (Narayanan et al., 2014). In the current study, water deficit increased root diameter in both bambara groundnut and groundnut. The current findings agree with findings by Qian et al. (2017) who found increase in root diameter under water stress. Furthermore, the current study revealed significant differences between species (bambara groundnut and groundnut) and within a

species (bambara groundnut) for root diameter. Fitter (1996); Judd et al. (2015), both reported similar findings, who revealed differences in root diameter under drought between and within species.

Root diameter is used to describe what the root and plant experience in the surrounding environment (Judd et al., 2015) and determines the rooting depth and ability to penetrate the soil (Ye et al., 2018). Thicker roots are known to go far into the deeper soil profile easily (Yu et al., 1995; Zheng et al., 2000; Bao et al., 2014) and hence improved water absorption (Richards et al., 2001). It is known that, thicker root diameter provides drought resistance in legumes (Purushothaman et al., 2013). In the present research, among the bambara groundnut landraces, S19-3 proved superiority over the other two bambara groundnut landraces (DodR and NALBAM 4) in terms of root diameter and volume. MNANJE (groundnut) is found to have thicker root diameter and larger root volume as compared to bambara groundnut landraces. This implies that, with larger root diameter and volume, such plants are able to exploit not only more water at a time but also nutrients. Therefore, in this context MNANJE is more favoured as compared to bambara groundnut landraces.

Root surface area

Water deficit stress reduced root surface area of both bambara groundnut and groundnut plants. Similar results has been reported in groundnut (Ding et al., 2013; Junjittakarn et al., 2014), in soybean (Zenis et al., 2016**),** while total root surface area in maize under drought was less changed (Qian et al., 2017). S19-3 had higher values of root surface area than DodR and NALBAM 4, which implies presence of numerous fine roots, and thus increased ability to reach more soil volume for increased water absorption during water deficit stress periods. In this study, bambara groundnut landraces DodR and NALBAM 4, showed a relatively higher

percentage decrease in root surface area under stress conditions as compared to S19-3. This implies that S19-3 is less affected by changes in soil moisture content and hence can survive under water deficit conditions.

Although MNANJE, showed highest values of root surface area, it showed a higher percentage decrease as compared to bambara groundnut landraces (with the exception of NALBAM 4 during flowering) (*Table 6.3.2*). This implies that, MNANJE is more affected in development of new roots (fine roots and root hairs) under water stress. However MNANJE, the groundnut, is favoured by its vigorous development of roots during early stages of its growth and helps in counteracting the drought occurring in early and late stages of plant growth (Ketrin and Reid, 1993). The reduction in root surface area found in both species could be attributed to limited capacity to develop fine roots and root hairs. It has been reported that, production of massive fine roots and root hairs increases surface area of roots (Lynch, 2011; Butare et al., 2011) and vice versa is true. Nevertheless, crops and or landraces with large root surface area are able to explore a larger volume of soil thus contributing to enhanced adaptation to soils under low moisture content and plant nutrients (Lynch, 2011, 2013; Rao et al., 2016). In the current findings, MNANJE and S19-3 were found to have relatively large surface areas and hence have the capacity to explore larger soil volumes. Exploiting large soil volume has an advantage of extracting more soil water under drought conditions. Therefore, MNANJE and S19-3 can thrive and give yields under water scarcity conditions.

Plant height and canopy spread

The effects of water deficit have been studied in different plants for development of different stress related indices. For example growth indices like plant height and canopy spread have been used in bambara groundnut (Mwale et al., 2007a; Vurayai et al., 2011a, b; Mabhaudhi

and Modi, 2013) and in groundnut (Arunachalam and Kannan, 2013; Madhusudan and Sudhakar, 2014b), black gram and green gram genotypes (Baroowa and Goigoi, 2012). It has been concluded that, water deficit stress in bambara groundnut (Mwale et al., 2007a; Mabhaudhi and Modi, 2013) and other crop plants including groundnut (Arunachalam and Kannan, 2013; Madhusudan and Sudhakar, 2014b) leads to reduced plant height and canopy spread. The present findings are in agreement with previous investigations. Reduced plant height and canopy spread are considered as mechanisms to reduce water consumption against insufficient water present in the soil (Mabhaudhi and Modi, 2013). Plants reduce canopy spread to increase water use-efficiency, although this has negative effects on economic yield potential (Blum, 2005).

The reduced plant height and canopy spread in both bambara groundnut and groundnut in the present study, may be because of mitotic sensitivity and decreased leaf expansion in drought conditions (Madhusudan and Sudhakar, 2014b). Insufficient water supply may affect cell division, elongation and enlargement as a result of low turgor, which might have ultimately led to the reduction in plant height and canopy spread (Sankar et al., 2007), in order to avoid excessive dehydration as an adaptive strategy by plants under moisture deficit stress conditions (Ratnakumar and Vadez, 2011).

Although DodR and MNANJE showed relative higher percentage decreases in plant height and canopy spread, in most cases MNANJE outweighed DodR. Reduced plant height and canopy spread is related to high WUE and reduced transpiration losses (Blum, 2005, 2009). The current findings can be explained in two ways; for DodR, higher percentage decrease in height and canopy spread was largely caused by stomatal closure (high WUE) whereas for MNANJE higher percentage decrease found in the two traits was largely associated with low stomatal

conductance (low transpiration). In the latter scenario, plants continue to transpire and photosynthesise at a slower rate by osmotic adjustment (OA). OA is the major plant adaptive reaction to drought in the smallest plants organs (cellular level) (Blum, 2005). OA has two major functions; maintains leaf turgor for the same leaf water potential under insufficient water thus supporting stomatal conductance under lower leaf water status (Sellin, 2001) and also it improves root capacity for water absorption (Chimenti et al., 2006). This OA is enhanced by accumulation of proline in leaves and other osmolytes (which in this context is not discussed), MNANJE showed significant accumulation of proline compared to DodR (see chapter 5). It can therefore be noted that, other crops/genotypes can photosynthesise, though at a slower rate, to give yields under water deficit stress conditions.

Root dry weight to shoot dry weight fraction

From the current study, higher values of root to shoot ratio were recorded in plants which were exposed to drought as compared to well-watered plants (*Table 6.3.4*). These results agree with findings by Vurayai et al. (2011a); Muhammad et al. (2015); Chibarabada et al. (2015a, b) who separately worked on bambara groundnut. Among the studied bambara groundnut landraces, S19-3 recorded the highest root to shoot ratio values. This correlates well with higher root volume and deeper roots shown by S19-3 (*Table 6.3.1*); which implies that the landrace is capable of exploiting deeper horizons for soil water. This also indicates higher distribution of biomass to roots. Variation in root:shoot dry weight ratio is suggested as a strategy associated with plants adjustments against water deficit conditions (Turner, 1986; Lee et al., 2016). It has been projected that crops respond to insufficient water supply by favouring roots with the available assimilates and hence higher root biomass (Wilson,

1988; Hasibeder et al., 2014). The increased belowground biomass could improve water absorption by the plants exposed to water deficit.

In the recent study, all plant materials that were exposed to water deficit stress showed higher root to shoot ratio as compared to well-watered plants. Higher values of root:shoot was due to the relatively greater reduction in shoot growth than in root growth rather than an increase in absolute root weight (Shrestha et al., 2005). Genotypes with a long taproot and more lateral roots have increased drought resistance and are being used for breeding high-yielding cultivars under water-limited conditions (Bandyopadhyay, 2014). Some bean cultivars have the capacity to modify the rhizosphere through surface root architecture and longer basal root hairs (particularly under stressed conditions) (Cisse and Amar, 2000). It has also been found that the root to shoot ratio in lentil increased by 14–100% compared with well-watered lentil when water deficits were imposed at the reproductive stage (Bandyopadhyay, 2014). The values of root to shoot ratio observed in MNANJE and S19-3 show that the two could perform better in dry areas because high values of root to shoot ratio have been considered as a trait for drought resistance strategy. Based on the results from the present study, MNANJE and S19-3 utilizes drought avoidance mechanism in adapting to conditions under insufficient soil water supply.

6.5 Conclusion

In this study, deepening of roots was the main root characteristic, which allowed both bambara groundnut and groundnut to overcome water deficit stress. Plants with deeper roots are associated with enhanced root biomass as well as high root length density which both favour absorption of water from the soil. Bambara groundnut landrace S19-3 and MNANJE, the groundnut, are good candidates for cultivation in dry areas due to their ability to

withstand water deficit stress through different drought resistance mechanisms. This study advanced our knowledge regarding physiological strategies against drought. Deeper roots, which allow extraction of water stored in the lower soil depths are important for crops grown in water limited environments. Identification of drought avoidance mechanisms displayed by both MNANJE and S19-3 and the rest of the results from the present study would be a useful contribution to breeding programmes aiming to identify and select superior plants root characteristics for drought conditions.

Technology development is key to future progress in root studies. Extraction of the entire root system from PVC columns to determine drought-induced changes in root architecture is laborious, inefficient and requires the destruction of plants. Furthermore, it is very difficult to recover all roots during washing.

CHAPTER SEVEN

General Discussion, Conclusion and Recommendations

7.1 Preamble

Crop plants experience drought stress due to an extended period of abnormally dry conditions in areas with below average rainfall and or water supply (Tekle and Alemu, 2016). Agriculture is the biggest consumer of water, accounting for 69% of all withdrawals worldwide and 21% in Europe and up to 82% in Africa (FAO, 2016a). Effects of climate change such as increases in temperature and insufficient soil moisture, are expected to be the major contributors to low yield of food crops by 2050 (FAO, 2016b). Major important cereals (wheat (*Triticum aestivum* L.), (maize (*Zea mays* L.), and rice/paddy (*Oryza sativa* L.) will be negatively affected by these changes (Ringler et al., 2010; Ray et al., 2013). Adaptation is increasingly seen as an inevitable answer to the challenges posed by climate change (Brassard and Singh, 2008). Among other efforts in searching for alternative solutions to combat effects of climate change, use of more drought resilience species has been suggested (Massawe et al., 2015; Mabhaudhi et al., 2016). Understanding of the drought resistance physiological mechanisms in bambara groundnut and groundnut is important in order to identify traits associated with drought resistance that can be included in crop improvement programmes.

7.2 Discussion

The current research studied the effects of water deficit stress on two legumes (groundnut (*Arachis hypogaea* L.) and bambara groundnut (*Vigna subterranea* L. Verdc). Both real field and rainout shelter experiments were carried out to explore the changes, adaptations and differences in the two species with respect to insufficient water supply during two growth

stages (flowering vs pod development). Findings from the current study are as described in the following subsections.

7.2.1 Crop phenology

Drought escape is among the strategies used by plants under water limited conditions to complete their growth period quickly during favourable conditions before unfavourable stressful conditions occur. In the present study, both bambara groundnut landraces and groundnut (MNANJE) showed a degree of phenological plasticity associated with drought escape mechanism by flowering and maturing early. Early flowering is considered as a means of escaping drought (Araus et al., 2002; Song et al., 2013). Drought escape strategy is mostly found in plants that have high metabolic rates with high cell expansion as well as cell development (Bodner et al., 2015). Improved photosynthesis rates as well as enhanced plant growth and development are consequences of higher rates of transpiration (Kooyers, 2015; Bodner et al., 2015). High rates of transpiration under water deficit were observed in S19-3 and MNANJE (Chapter 5), which implies rapid crop development (early flowering and maturing) and hence employing escape drought mechanism in adapting to water deficit conditions. The current findings showed that, genetic differences exist among bambara groundnut landraces in the timing of phenological stages. Moreover, it was found that groundnut, in this case MNANJE, showed clear differences in days to attain different phenological stages compared to bambara groundnut landraces. MNANJE is therefore better adapted to the specific drought conditions than bambara groundnut landraces under current investigation. Promoting potential bambara groundnut landraces/genotypes/varieties, in this case S19-3, will not only improve the food security to small holder famers but also their economy.

7.2.2 Relative water content

Low relative water content, which occurs due to water deficit has been reported to decrease plant growth and development, inhibits dry matter accumulation and accelerates leaf senescence, decreases photosynthesis, increases the frequency of zygotic abortion and decreases grain number, size and final yield (Sikuku et al., 2010b). Regardless of the significant decreases in RWC revealed in the current study, both bambara groundnut and groundnut, showed the capability of maintaining appreciable amount of RWC (Chapter 4 – 5). The RWC under water deficit stress in bambara groundnut ranged between 60% and 66% whereas for groundnut it ranged between 72% and 74%. Maintenance of higher RWC under drought indicates the species' ability to resist water stress (Li et al., 2011). As it can be observed from the results (Chapters 4 - 5), MNANJE maintained higher values of RWC compared to S19-3 which was superior among the bambara groundnut landraces. RWC in plants can be regarded both as an indicator of water scarcity and as an important criteria in selection/screening of drought resistance genotypes and or species. In order for RWC trait to be effective with in mitigating negative impacts associated with global warming, it must not be considered alone. Combination of drought resistance traits is crucial in combating effects of current and future rainfall and temperature variability.

7.2.3 Gaseous exchange

Insufficient supply of water to plants is known to reduce stomatal aperture resulting to full stomatal closure (Chaves et al., 2003; Mabhaudhi et al., 2012). Current research, showed that, water deficit reduced transpiration and photosynthesis and consequently decreases final economic yield. In bambara groundnut landraces, the extent of such reductions were landrace specific, whereby S19-3 was least affected. Comparing the two species, MNANJE the

groundnut, showed the smallest decrease in stomatal conductance. The relatively greater degree of reduction in gaseous exchange shown by NALBAM 2, NALBAM 4 and DodR (Chapters 4 – 5) implies an ability to improve water use by reduced transpiration losses, an adaptation related to drought avoidance mechanisms (Turner et al., 2001; Basu et al., 2016). Nonetheless this adaptation is not beneficial for yield production. This suggests that bambara groundnut landraces down regulate their photosynthesis under water scarce conditions at expense of yield. Blum (2005, 2009) suggested that, for beneficial drought adaptation, plants should maintain their high levels of transpiration while enhancing soil water capture. Although the chlorophyll content index of the landrace S19-3 was reduced, its photosynthesis was backed up by accumulation of proline (Chapter 5) and its ability for root penetration to the deeper horizons (Chapter 6). In this context, MNANJE showed the ability to withstand drought by its ability to photosynthesise even under water deficit conditions. This suggests that MNANJE does not close stomata completely even under severe water stress. This is evidenced in conditions where MNANJE showed more pronounced signs of wilting as compared to bambara landraces, but still recorded relatively high rates of photosynthesis and transpiration (Chapter 5). Although from different species, both S19-3 and MNANJE can be utilized in semi-arid areas to boost the economy and food security of the farmers.

7.2.4 Chlorophyll content index

Water deficit has also been found to impair metabolic activities (Lawson et al., 2003). Water deficit enhances production of free radicals, specifically those containing oxygen. These oxygen reactive species (ROS) negatively affect proteins and activates chlorophyllase, an enzyme responsible for chlorophyll production (Farooq et al., 2009; Fathi and Tari, 2016). In the current study, chlorophyll content index was used to evaluate the drought resistance

(Efeoglu et al., 2009) of bambara groundnut and groundnut landraces. Higher content of chlorophyll is generally associated with higher resistance to drought (Li et al., 2006; Guo et al., 2009). Current findings for bambara groundnut landraces showed reduced chlorophyll content index under water limited conditions (Chapter 4 and 5). The decrease in chlorophyll content shown by bambara groundnut is associated with a strategy to resist drought. Surprisingly, Nautiyal et al. (2017), found increases in chlorophyll content in S19-3 under water deficit stress and explained it as an indication of greater strength shown by photosynthesis pigment (carotenoid) in S19-3. Leaving aside the effect of water deficit on chlorophyllase, Mabhaudhi (2012) explained that, reduction in chlorophyll content, also implies energy dissipation as a stress resistance mechanism. Contrary to bambara groundnut landraces, chlorophyll content index in MNANJE increased under water deficit conditions (Chapters 4 – 5). Furthermore, MNANJE was found to have higher values of chlorophyll content index in all water regimes as compared to bambara groundnut landraces. The current results suggests that, chlorophyll content may be a good trait in assessing drought resistance in bambara groundnut and groundnut as well as its application to other crops.

7.2.5 Proline

Proline accumulation is a common metabolic reaction of plants to environmental (abiotic) as well as non-environmental (biotic) difficulties. Proline accumulation has been reported in crops under insufficient water supply (Yamada et al., 2005; Muhammad et al., 2015) and water deficit stress in bambara groundnut (Vurayai et al., 2011a), maize (Mohammadkhani and Heidari, 2008) and wheat (Cattivelli et al., 2000). Proline accumulation during growth of plants has been associated with response to abiotic and biotic stresses (Kaur and Asthir, 2015). Its accumulation reduces the toxic effects of free radicals formed due to the water deficit

(Baskaran and Muruganandam, 2017). Proline is considered as a scavenger of oxygen containing free molecules (reactive oxygen species [ROS]) and capable of reducing the allied injuries (Rejeb et al., 2014; Viehweger, 2014; Kaur and Asthir, 2015). It has been reported that proline accumulation in stressed plants is a resistance mechanism (KaviKishor and Sreenivasulu, 2014; Baskaran and Muruganandam, 2017).

In the present study proline content of all landraces increased due to water deficit stress. The current findings agree with previous observations in bambara groundnut (Vurayai et al., 2011a), blackgram, green gram (Barrowa and Goigoi, 2012; Baskaran and Muruganandam, 2017), in chickpea (Mafakheri et al., 2010) and groundnut (Sharada and Naik, 2011). In the present research, evaluation of proline content in bambara groundnut and groundnut under water deficit stress (Chapter 5) revealed that, among bambara groundnut landraces, S19-3 accumulated the highest proline content followed by DodR and lastly NALBAM 4. MNANJE, the groundnut, showed the higher values of proline as compared to S19-3. Increased concentration of osmolytes (such as proline) has been suggested as a trait for screening for water deficit resistance (Jaleel et al., 2007). Under insufficient water conditions, proline serves as a redox-buffer as well as osmoprotectant (KaviKishor and Sreenivasulu, 2014; Baskaran and Muruganandam, 2017). An increase in proline content is a positive indicator of salinity and drought resistance (Yaish, 2015). Accumulation of proline has been suggested to contribute to stress resistance by acting as the molecular chaperons and maintain the protein integrity, hence enhancing the functions of various enzymes. The higher values of proline content observed in S19-3 and MNANJE, implies that the two landraces are able to overcome the negative consequences of ROS and excessive heat in drought environments (Rejeb et al., 2014), also are able to maintain cell turgor and stabilizing membranes against drought. Based

on these observations therefore, S19-3 and MNANJE can be regarded as drought resistant. Therefore, identification of the potential of these two landraces against drought is a good news to famers in drought prone areas. Researchers/plant breeders are now aware of which plant parts or traits to more focus on in improving these two species, while on the other hand, farmers can be informed on the ability of the two landraces and start utilizing them.

7.2.6 Roots traits

The earliest plant part(s) that recognise and react to water scarcity conditions are roots (Fenta et al., 2014). Roots are very important in both absorption of soil water and nutrients by plants (Paez-Garcia et al., 2015). Studies relating to plant roots have been reported widely (Nardini et al., 2002; Sperry et al., 2002; Songsri et al., 2008; Polania et al., 2016, 2017). Though, the role of roots in maintaining biomass as well as final harvests exposed to insufficient water supply are still not clearly understood (Polania et al., 2017). Various patterns/combination (ideotypes) of roots are suggested to combat drought related problems (Yang et al., 2013; Rao et al., 2016). Steep, cheap and deep roots is among ideotypes suggested for optimization of soil moisture and nitrogen for adaptation to abiotic stresses (Lynch, 2013). Early root vigour, large root volume, large surface area and greater water uptake via enhanced transpiration are part of the steep cheap and deep ideotype. Below ground assessment of common bean under drought conditions revealed deep rooting as an important trait for absorption of soil moisture in deeper layers (Rao, 2014; Burridge et al., 2016). Furthermore, Pirnajmedin et al. (2015) reported that, plants achieve drought resistance mechanisms through well-developed and expanded or deep root systems. In the present study, root systems of the studied landraces responded differently to water deficit stress. Basing on the current root evaluation results, MNANJE and S19-3 utilizes both avoidance and tolerance drought mechanisms in adaptation

to drought conditions. Thus, these two legumes can be employed in breeding programmes in efforts to couple with the predicted environmental threats.

7.2.7 Summary of observed mechanisms and traits

In the current study, all three drought resistance strategy mechanisms were revealed. *Figure 7.2.1* summarises the strategies and phenotypes/traits involved and their effect on yield.

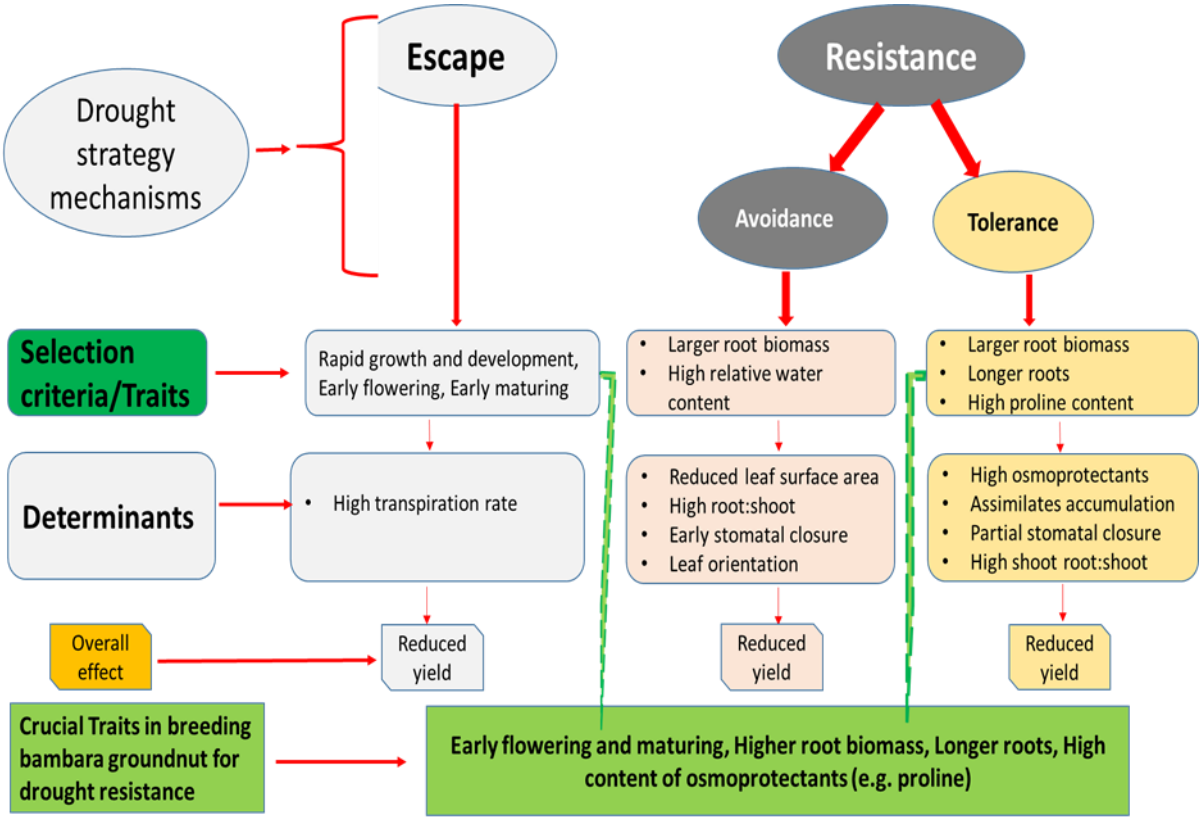


Figure 7.2.1: Description of drought strategy mechanisms and traits observed in different bambara groundnut landraces.

7.3 Conclusion

The current study explored the traits and drought mechanisms in bambara groundnut and groundnut. The drought adapting mechanisms differed among bambara groundnut landraces. NALBAM 2, NALBAM 4 and DodR showed only avoidance drought mechanism. On the other hand, bambara groundnut landrace, S19-3 involved combination of escape, avoidance and tolerance drought mechanisms same as those expressed by MNANJE, the groundnut. Roots

and leaves are equally important parameters in bambara groundnut and groundnut adaptation to drought. Drought avoidance was achieved by closing stomata, loss of chlorophyll, reduced canopy size and deep roots. Drought escape was achieved through phenological plasticity, where by MNANJE and S19-3 was found to flower and reach physiological maturity earlier. Drought tolerance mechanisms were achieved through high accumulation of proline and deeper roots. Grain yield in both species were reduced because of drought, whereas drought enhanced WUE in bambara groundnut and decreased with water deficit stress in groundnut. S19-3 showed adaptability to production under water limited conditions as compared to DodR and NALBAM 4. Generally, MNANJE, the groundnut showed superiority in adaptation to water deficit stress as compared to bambara groundnut landraces and hence minimal yield losses.

Although S19-3 and MNANJE belong to different species, both share almost the same traits for drought resistance. S19-3 and MNANJE, the groundnut, were found to have relatively small reductions in gaseous exchange (avoidance mechanism), high values of proline for osmoprotection (tolerance mechanism) and matured early (escape mechanism). Furthermore, both had deeper roots for water extraction from deeper horizons (avoidance and or tolerance mechanism). The two can be suitable for cultivation in areas with limited soil moisture content and still produce some yields. The potential shown by MNANJE and S19-3 suggests that, breeding for drought resistance genotypes for improved food security is possible. The two landraces can also be employed in both crop diversification and intensification for mitigating current and future effects of climate change. Through crop intensification and diversification by incorporating these legumes into cropping system (N-fixation, soil fertility improvement), yields of other crops will increase. Furthermore, S19-3 can be directly utilized as food and through value addition, other products can be made from

it and hence source of income. MNANJE is mostly used as snack, but it is a major source of oil and other products like peanut butter, whereby from the sales of these products the economy of farmers will be improved. The observations from this study provide useful information for genetic improvement of bambara groundnut and groundnut for drought resistance for increased yield.

7.4 Key observations and recommendations

Bambara groundnut performs better under warm environments. In the course of the field investigations some bambara groundnut landraces (e.g. NALBAM 2, NALBAM 4) failed partly due to low temperature (<16 ^{o}C) while others (e.g. S19-3) showed some resistance to low temperatures. Groundnut, MNANJE was not affected. It is suggested therefore, to conduct parallel studies (both in real field and control environments) to study the influence of temperature, insufficient water supply and their interaction in bambara groundnut and groundnut.

Limited information exist on how bambara groundnut root system react to water deficit stress. The present study points to the potential of roots in drought resistance mechanisms in bambara groundnut and groundnut. Future drought related studies in bambara groundnut as an underutilized and neglected crop, should also include the underground part/roots.

Although bambara groundnut and groundnut are from different species, they share a lot of characteristics ranging from mode of drought adaptability to reproductive features. Literature reviews revealed only a very few studies comparing the two legumes. Therefore, future research on drought resistance is encouraged to include evaluating and comparing (between

the two species) using a diverse range of landraces/genotypes of both bambara groundnut and groundnut.

Although bambara groundnut is reported to be relatively less affected by diseases and pests (Linnemann and Azam-Ali, 1993; Tweneboah, 2000), in the present study it was not the case. In the three field experiments, in Tanzania, both bambara groundnut and groundnut were not attacked by pests and did not show any symptoms of diseases. However, the two seasons rainout shelter experiments conducted in Nottingham University Malaysia, some cases of fungal infections and leaf spot were observed in bambara groundnut landraces but not in groundnut. Effa and Uko (2017) reported severe viral leaf curl disease incidence under high humidity conditions that resulted in drastic yield reductions in bambara groundnut. This calls for further studies on pests and diseases in bambara groundnut and groundnut under differing environments and locations. It will be worth to also compare bambara groundnut with other legumes.

References

Abate, T., Alene, A. D., Bergvinson, D., Shiferaw, B., Silim, S., Orr, A. and Asfaw, S. (2012). Tropical Grain Legumes in Africa and South Asia: Knowledge and Opportunities. SAT (https://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/health/ (Site visited on 15 June 2019).

Abejide, D. R., Falusi, A., Gana, A. S., Adebola, M. O., Daudu, O. A. Y. and Salihu, B. Z. (2018). Evaluation of Seed Yield of Nigerian Bambara Groundnut [Vigna subterranea (L.) Verdc] Landraces under Varying Water Conditions. Not Sci Biol, 2018, 10(2):233-239. DOI: 10.25835/nsb10210238.

Adeboye, A. S. and Emmambux, M. N. (2017). Physicochemical, morphological, thermal and pasting properties of marama (Tylosema esculentum) storage root starch. Starch-Starke, 69 pp. 1-9.

Adegbola, O. B. J. and Bamishaiye, E. (2011). Bambara groundnut: an under-utilized nut in Africa. Advances in Agricultural Biotechnology. 1; 60 –72.

Ademiluyi, Y. S., Oyelade, O. A., Jaes, D. and Ozumba, I. C. (2011). Performance evaluation of a tractor drawn groundnut digger/shaker for agricultural productivity. *Tillage for Agriculture Productivity and Environmental Sustainability Conference*, February 21 – Jideani, V. A. and Diedericks, C. F. (2014). Nutritional, therapeutic, and prophylactic properties of Vigna subterranea and Moringa oleifera. In: Oguntibeju O (Ed), Antioxidant-antidiabetic agents and human health. Intech Publishers, pp: 22.

Adhikari, U., Nejadhashemi, A. P. and Woznicki, S. A. (2015). Climate change and eastern Africa: a review of impact on major crops. Food and Energy Security. 4(2); 110 – 132.

Adinya, I. B., Enun, E. E. and Ijoma, J. U. (2010). Exploring profitability potentials in groundnut production through agroforestry practices: a case study in Nigeria. *Journal of Animal and Plant Sciences* 20(2): 123 – 131.

Admasu, R., Asefa, A. and Tadesse, M. (2019). Effect of Growth Stage Moisture Stress on Common Bean (*Phaseolus Vulgaris L*.) Yield and Water Productivity at Jimma, Ethiopia. Int J Environ Sci Nat Res 16(1): p8. IJESNR.MS.ID.555929.

Adzawla, W., Donkoh, S.A., Nyarko, G., O'Reilly, P., Olayide, O. E. and Awai, P. E. (2015). Technical efficiency of bambara groundnut production in Northern Ghana. UDS International Journal of Development [UDSIJD] Volume 2 No. 2; 37 – 49.

Agbicodo, E. M., Fatokun, C. A., Muranaka, S., Visser, R. G. F. and van der Linden, C. G. (2009). Breeding drought tolerant cowpea: Constraints, accomplishments, and future prospects. *Euphytica*, *167*, 353–370.

AghaKouchak, A., Feldman, D., Hoerling, M., Huxman, T. and Lund, J. (2015). Water and climate: Recognize anthropogenic drought. *Nature* 524, 409–411.

AGRA (Alliance for a Green Revolution in Africa). (2014). Africa Agriculture Status Report: Climate change and smallholder agriculture in sub Saharan Africa. Nairobi, Kenya. http://www.agra.org/our-results/agra-statusreports (last accessed 28.03.2018.).

Akibode, S. and Maredia, M. (2011). Global and Regional Trends in Production, Trade and Consumption of Food Legume Crops. Department of Agricultural, Food and Resource Economics: Michigan State University.

Akkaseng, C., Vorasoot, N., Jogloy, S. and Patanotai, A. (2003). Relationship between SPAD readings and chlorophyll contents in leaves of peanut (*Arachis hypogaea* L). *Thai Journal of Agricultural Science* 36 (3), 279–284.

Al Shareef, I. (2010). The effect of temperature and drought stress on bambara groundnut (Vigna subterranea (L.) Verdc) landraces. MSc Thesis. University of Nottingham. p282.

Al Shareef, I., Sparkes, D. and Azam-Ali, S. (2013). Temperature and drought stress effects on growth and development of bambara groundnut (Vigna subterranea L.). Exp. Agric., 50, 72–89.

Al Shareef, I., Sparkes, D. and Azam-Ali, S. (2014). Temperature and drought stress effects on growth and development of bambara groundnut (V*igna subterranea* l.) *Expl Agric.* Volume 50 (1), pp. 72–89 doi:10.1017/S0014479713000379.

Alaei, Y. (2011). The effect of amino acids on leaf chlorophyll content in bread wheat genotypes under drought stress conditions. Middle-East Journal of Scientific Research, 10(1), 99–101.

Alexandratos, N. and Bruinsma, J. (2012). World Agriculture Towards 2030/2050. The 2012 Revision. ESA Working Paper No. 12-03. Rome: Food and Agriculture Organization, Agricultural Development, Economics Division.

Ali, S., Liu, Y., Ishaq, Shah, T., Abdullah, Ilyas, A. and Din, I. U. (2017). Climate Change and Its Impact on the Yield of Major Food Crops: Evidence from Pakistan. Foods, 6, 39; 1 -19.

Aliyu, S. and Massawe, F. J. (2013). Microsatellites based marker molecular analysis of Ghanaian bambara groundnut (Vigna subterranea (L.) Verdc) landraces alongside morphological characterization. Genet Resour Crop Evol 60:777–787.

Allen, L. H. Jr., Boote, K. J. and Hammond, L .C. (1976). Peanut stomatal diffusive resistance affected by soil water and solar radiation. Proc. Soil Crop Sci. Soc. Fla. 35: 42—46.

Amarteifio, J. O., Tibe, O. and Njogu, R. M. (2006). The mineral composition of Bambara groundnut (Vigna subterranea (L) Verdc) grown in southern Africa. African Journal of Biotechnology, 5, 2408–2411.

Aminian, R., Mohammadi, S., Hoshmand, S. and Khodombashi, M. (2011). Chromosomal analysis of photosynthesis rate and stomatal conductance and their relationships with grain yield in wheat (Triticum aestivum L.) under water-stressed and well-watered conditions. Acta Physiol Plant 33(3):755–764.

Amoroso, G., Frangi, P., Piatti, R., Ferrini, F., Fini, A. and Faoro, M. (2010). Effect of container design on plant growth of Littleleaf Linden and field elm. *HortScience*, *45*, 1824 - 1829.

Anjum, F., Yaseen, M., Rasul, E., Wahid, A. and Anjum, S. (2003). Water stress in barley (*Hordeum vulgare* L.). *J. Agric. Sci.* 40: 43–44.

Anjum, S. A., Farooq, M., Wang, L. C., Xue, L. L., Wang, S. G., Wang, L., Zhang , S. and Chen, M. (2011). Gas exchange and chlorophyll synthesis of maize cultivars are enhanced by exogenously applied glycinebetaine under drought conditions. Plant Soil Environ. 577, 326–331.

Ao, J., Fu, J., Tian, J., Yan, X. and Liao, H. (2010). Genetic variability for root morph-architecture traits and root growth dynamics as related to phosphorus efficiency in soybean. *Funct. Plant Biol.*, *37*, 304–312.

Appleby, P. N. and Key, T. J. (2016). The future of animal products in the human diet: health and environmental concerns: The long-term health of vegetarians and vegans Proceedings of the Nutrition Society. (75) 287–293. doi:10.1017/S0029665115004334.

Arakama, N. K. (2013). Profitability of intercropping corn with mung bean and peanut. *Journal of Peanut* 17(1): 65 – 70.

Araki, H., Morita, S., Tatsumi, J. and Iijima, M. (2002). Physiomorphological analysis on axile root growth in upland rice. Plant Production Science 5,286–293.

Araújo, S. S., Beebe, S., Crespi, M., Delbreil, B., González, E. M., Gruber. V., Lejeune-Henaut, I., Link, W., Monteros, M. J., Prats, E., Rao, I., Vadez, *V.* and Vaz, Patto, M. C. (2014). Abiotic stress responses in legumes: strategies used to cope with environmental challenges. Crit Rev Plant Sci.; 34:237–280.

Araus, J. L. and Cairns J. E. (2014). Field high-throughput phenotyping: the new crop breeding frontier.Trends Plant Sci. 2014; 19:52–61.

Araus, J. L. and Cairns, J. E. (2013). Field high-throughput phenotyping: The new crop breeding frontier. *Trends Plant Sci.*, 19, 1–62.

Araus, J. L., Slafer, G. A., Reynolds, M. P. and Royo, C. (2002). Plant breeding and drought in C3 cereals: what should we bread for? Ann. Bot. 89, 925–940.

Arunachalam, P. and Kannan, P. (2013). Screening for Drought Tolerant Groundnut (*Arachis hypogaea* L.) Lines Suitable for Rainfed Alfisol. Asian J. Agric. Res. 7(1):35-42.

Arunyanark, A., Jogloy, S., Akkasaeng, C., Vorasoot, N., Kesmala, T., Nageswara Rao, R. C., Wright, G. C. and Patanothai, A. (2008). Chlorophyll stability is an indicator of drought tolerance in peanut.J Agron Crop Sci 194:113–125.

Arunyanark, A., Jogloy, S., Wongkaew, S., Akkasaeng, C., Vorasoot, N., Wright, G. C., Rachaputi Rao, C. N., and Patanothai, A. (2009). Association between aflatoxin contamination and drought tolerance traits in peanut. Field Crops Research,Vol. 114, 2009, 14-22.

Arve, L. E., Torre, S., Olsen, J. E. and Tanino, K. K. (2011). Stomatal responses to drought stress and air humidity. In: Abiotic Stress in Plants – Mechanisms and Adaptations, Shanker A (Ed.), InTech Publication, pp. 267–280.

Asch, F., Becker, M. and Kpongor, D. S. (2005). A quick and efficient screen for tolerance to iron toxicity in lowland rice. J. Plant Nutr. Soil Sci. 168, 764-773.

Asif, M. and Kamran, A. (2011). Plant breeding for water-limited environments. Crop Sci. 51:2911–2912. doi:10.2135/cropsci2011.12.0004br.

Atkinson, N. J., Lilley, C. J. and Urwin, P. E. (2013). Identification of Genes Involved in the Response of Arabidopsis to Simultaneous Biotic and Abiotic Stresses. Plant Physiology, 162(4):2028–2041.

Atoyebi, J. O., Oyatomi, O., Osilesi, O., Adebawo, O. and Abberton, M. (2017). Morphological Characterisation of Selected African Accessions of Bambara Groundnut (*Vigna subterranea* (L.) Verdc). International Journal of Plant Research, 7(2): 29-35. DOI: 10.5923/j.plant.20170702.01.

Azam-Ali S. N., Sesay, A., Karikari, S., Massawe, F. J., Aguilar-Manjarrez, J., Bannayan, M. and Hampson, K. J. (2001). Assessing the potential of an underutilized crop – a case study using bambara groundnut. *Explor. Agric.* 37 433–472.

Bacon, M. A. (2004). Water use efficiency in plant biology. Oxford, UK: Blackwell Publishing. p. 327.

Ballantyne, J. S. and Chamberlin, M. E. (1994). Regulation of cellular amino acid levels. In "Cellular and Molecular Physiology of Cell Volume Regulation" (K Strange ed), CRC Press, Boca Raton, pp. 111-122.

Bamishaiye, O. M., Adegbola, J. A. and Bamishaiye, E. I. (2011). Bambara groundnut: an under-utilized nut in Africa. Adv Agric Biotechnol 1: 60-72.

Bandyopadhyay, P. K. (2014). Root distribution pattern of pulses in response to water availability. In 'Resource conservation technology in pulses'. (Eds PK Ghosh, N Kumar, MS Venkatesh, KK Hazra, N Nadarajan) Scientific Publishers: Jodhpur, India, pp. 483–493.

Banon, S. J., Ochoa, J., Franco, J. A., Alarcon, J. J. and Sanchez-Blanco, M. J. (2006). Hardening of oleander seedlings by deficit irrigation and low air humidity. Environ. Exp. Bot. 56: 36-43.

Bao, Y., Aggarwal, P., Robbins, N. E., Sturrock, C. J., Thompson, M. C., Tan, H. Q., Tham, C., Duan, L., Rodriguez, P. L., and Vernoux, T. (2014). Plant roots use a patterning mechanism to position lateral root branches toward available water. Proc. Natl. Acad. Sci. USA; 111, 9319–9324.

Barnabás, B., Jäger, K. and Fehér, A. (2008). The effect of drought and heat stress on reproductive processes in cereals. Plant Cell Environ. 31, p11–38.

Baroowa, B. and Gogoi, N. (2012). Effect of induced drought on different growth and biochemical attributes of blackgram (Vigna mungo L.) and green gram (Vigna radiata L.). J Environ Res Dev 6:584-593.

Barrs, H. D. and Weatherley, P. E. (1962). A re-examination of the relative turgidity technique for estimating water deficits in leaves.Australian Journal of Biological Sciences, 15:413-428.

Baskaran, A. and Muruganandam, A. (2017). Enhancing Role of Proline in Scavenging Free Radicals by Antioxidative Defence System during Stress in Black Gram and Cluster Bean. Int. J. Pharm. Sci. Rev. Res., 43(1), Article No. 40, Pages: 211-216 ISSN 0976 – 044X.

Basu, S., Mayes, S., Davey, M., Roberts, J. A., Azam-Ali, S. N., et al. (2007a) Inheritance of 'domestication' traits in bambara groundnut (Vigna subterranea (L.) Verdc). Euphytica 157(1-2): 59-68.

Basu, S., Ramegowda, V., Kumar, A. and Pereira, A. (2016). Plant adaptation to drought stress. *F1000Research*, p1-10. doi: 10.12688/f1000research.7678.1.

Basu, S., Roberts, J.A., Azam-Ali, S. N. and Mayes, S. (2007b). Bambara groundnut. In: Kole C (Ed) Genome mapping and molecular breeding in plants. Pulses, Sugars and Tuber Crops, vol 3. Springer, Berlin.

Bates, L. S., Waldren, R. P. and Teare, I. D. (1973). Rapid determination of free proline for water-stress studies. Plant Soil 39: 205- 207.

Battisti, D. and Naylor, R. L. (2009). Historical warnings of future food insecurity with unprecedented seasonal heat. Science 323:240–244.

Baudoin, J. P. and Mergeai, G. (2001). Grain Legumes in Crop production in Tropical Africa. P. 313 – 317.

Beebe, S. E., Rao, I. M., Blair, M. W and Acosta-Gallegos, J. A. (2013). Phenotyping common beans for adaptation to drought. Front, Physiol. 4, 35.

Begemann, F. (1988). Eco geographic differentiation of bambara groundnut (*Vigna subterranea)* in the collection of the International Institute of Tropical Agriculture (IITA). Giessen, Wissenschaftlicher Fachverlag Germany. p153.

Belachew, K. Y., Nagel, K. A., Fiorani, F. and Stoddard, F, L. (2018). Diversity in root growth responses to moisture deficit in young faba bean (*Vicia faba* L.) plants. PeerJ 6:e4401 https://doi.org/10.7717/peerj.4401.

Benjamin, J. G. and Nielsen, D. C. (2004). A method to separate plant roots from soil and analyze root surface area. *Plant Soil*, *267*, 225–234.

Benjamin, J. G. and Nielsen, D. C. (2006). Water deficit effects on root distribution of soybean, field pea and chickpea. Field Crops Research 97: p248-253. DOI 10.1016/j.fcr.2005.10.005.

Berchie, J. N., Opoku, M., Adu-Dapaah, H., Agyemang, A., Sarkodie-Addo, J., Asare, J., Addo, J. and Akuffo, H. (2012). Evaluation of five bambara groundnut (Vigna subterranea (L.) Verdc) landraces to heat and drought stress at Tono Navrongo, Upper East Region of Ghana. African Journal of Agricultural Research Vol.7 (2), pp. 250-256.

Berchie, J., Sarkodie-Addo, J., Adu-Dappah, H., et al. (2010). Yield Evaluation of Early Maturity Bambara Groundnut (Vigna subterranea L. Verdc) Landraces at the CSIR-Crops Research Institute, Fumesua-Kumasi, Ghana. J Agron 9:175–179.

Berger, B., Parent, B. and Tester, M. (2010). High-throughput shoot imaging to study drought responses. *Journal of Experimental Botany*, Volume 61, Issue 13, p3519–3528, https://doi.org/10.1093/jxb/erq201.

Berkowitz, G. A. (1998). Water and Salt Stress. In: Photosynthesis: A Comprehensive Treatise, Raghavendra, A. S. (Ed.). Cambridge University Press, Cambridge, UK., pp: 226-237.

Bernier, J., Kumar, A., Venuprasad, R., Spaner, D., Verlukar, S., Mandal, N. P., Sinha, P. K., Peeraju, P., Dongre P. R., Mahto, R. N. and Atlin, G. N. (2009). Characterization of the effect of rice drought resistance qtl12.1 over a range of environments in the Philippines and eastern India. Euphytica 166:207–217.

Bioversity International (2011). "Plant Genetic Resources Accession Level Data Provided by: International Institute of Tropical Agriculture (IITA)". www.genesys-pgr.org.

Bishop, J., Potts, S. G. and Jones, H. E. (2016). Susceptibility of faba bean (Vicia faba L.) to heat stress during floral development and anthesis. J. Agron Crop Sci. 202, 508–517. doi: 10.1111/jac.12172.

Bita, C. E. and Gerats, T. (2013). Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat tolerance crops. Front. Plant Sci. 4:273. doi: 10.3389/fpls.2013.00273.

Black, C. A. (1965). Methods of soil analysis. Part I, American Society of Agronomy. Madison, Wisconsin, USA. p1572.

Bloom, A. J., Zwieniecki, M. A., Passioura, J. B., Randall, L. B., Holbrook, N. M. and Clair, D. A. (2004). Water relations under root chilling in a sensitive and tolerant tomato species. Plant, Cell and Environment. vol. 27, No. 8, p. 971–979.

Blum, A. (1997). Crop response to drought and the interpretation of adaptation. In: E. Belhassen (*ed*) *Drought tolerance in higher plants*. Kluwer Academic Publisher.

Blum, A. (2005). Drought resistance, water-use efficiency, and yield potential – are they compatible, dissonant, or mutually exclusive? Australian Journal of Agricultural Research 56, 1159-1168.

Blum, A. (2009). Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. *Field Crop Res.* 112,119–123.doi:10.1016/j.fcr.2009.03.009.

Blum, A. (2011). *Plant Breeding for Water-limited Environments*. New York, NY: Springer Science +Business Media.doi:10.1007/978-1-4419-7491-4.

Bodner, G., Nakhforoosh, A., and Kaul, H. P. (2015). Management of crop water under drought: a review. Agron. Sustain. Dev. 35, 401–442. doi: 10.1007/s13593- 015-0283-4.

Boese, S. R., Wolfe, D. W. and Melkonian, J. J. (1997). Elevated CO2 mitigates chilling-induced water stress and photosynthetic reduction during chilling. Plant, Cell and Environment. vol. 20, No. 5, p625–632.

Bonfante, A., Terribile, F. and Bouma, J. (2019). Refining physical aspects of soil quality and soil healthwhen exploring the effects of soil degradation andclimate change on biomass production: an Italian case study. SOIL, 5, 1–14.

Bonthala, V. S., Mayes, K., Moreton, J., Blythe, M., Wright, V., May, S. T., Massawe, F., Mayes, S. and Twycross, J. (2016). Identification of Gene Modules Associated with Low Temperatures Response in Bambara Groundnut by Network-Based Analysis. PLoS ONE 11(2); p18. e0148771. doi:10.1371/journal.pone.0148771.

Boontang, S., Girdthai, T., Jogloy, S., Akkasaeng, C. Vorasoot, N., Patanothai, A. et al. (2010). Responses of released cultivars of peanut to terminal drought for traits related to drought tolerance. Asian Journal of Plant Science 9:423-431. doi:10.3923/ ajps.2010.423.431.

Boote, K. J. (1982). Growth Stages of Peanut (Arachis hypogaea L.). Peanut Science: January 1982, Vol. 9, No. 1, pp. 35-40.

Boote, K. J. and Ketring, D. L. (1990). Peanut. In: Stewart B.A. and Nielson D.R. (eds), Irrigation of Agricultural Crops. ASA- CSSA-SSSA, Madison.

Borrell, A. K., Mullet, J. E., George-Jaeggli, B., van Oosterom, E. J., Hammer, G. L., Klein, P. E. and Jordan, D. R. (2014). Drought adaptation of stay-green sorghum is associated with canopy development, leaf anatomy, root growth, and water uptake. J. Exp. Bot. 65:6251–6263. doi:10.1093/jxb/eru232.

Bouma, T. J., Nielson, K. L. and Koutstaal, B. (2000). Sample preparation and scanning protocol for computerized analysis of root length and diameter. Plant Soil. 218: 185-196.

Boyer, J. S. (1982). Plant productivity and environment. Science 218: 443-448.

Brassard, J. P. and Singh, B. (2008). Impacts of climate change and CO2 increase on agricultural production and adaptation options for Southern Québec, Canada. *Mitig. Adapt. Strateg. Glob. Change*; *13*: 241–265.

Brink, M., Ramolemana, G. M and Sibuga, K. P. (2006). *Vigna subterranea* (L.) Verdc In Brink, M. and Belay, G. (Editors). Plant Resources of Tropical African 1. Cereals and pulses. PROTA Foundation, Wageningen, Netherlands. pp. 213-218.

Brodribb, T. J. and McAdam, S. A. M. (2011). Passive origins of stomatal control in vascular plants. Science 331: 582-585.

Burridge, J. D., Jochua, C. N., Bucksch, A. and Lynch, J. P. (2016). Legume shovelomics: high-throughput phenotyping of common bean (*Phaseolus vulgaris* L.) and cowpea (Vigna unguiculata subsp, unguiculata) root architecture in the field. F Crop Res 192:21–32. doi: 10.1016/j.fcr.2016.04.008

Busch, F. A. (2014). Opinion: the red-light response of stomatal movement is sensed by the redox state of the photosynthetic electron transport chain. Photosynth Res 119(1–2):131–140.

Butare, L., Rao, I., Lepoivre, P., Polania, J., Cajiao, C., Cuasquer, J. and Beebe, S. (2011). New genetic sources of resistance in the genus Phaseolus to individual and combined aluminium toxicity and progressive soil drying stresses. Euphytica. 181(3):385–404.

Carvalho, J. J., Saad, J. C. C., Teixeira, M. B., Júnior, J. A., Melissa Selaysim Di Campos, M. S., Horschutz, A. C. O. and Cunha, F. N. (2016). Growth and production of common bean in direct seeding under irrigated deficit condition. African Journal of Agricultural Research. Vol. 11(31), 2841 – 2848. DOI: 10.5897/AJAR2016.11106.

Castle, S. L., Thomas, B. F., Reager, J. T., Rodell, M., Swenson, S. C. and Famiglietti, J. S. (2014). Groundwater depletion during drought threatens future water security of the Colorado River Basin. Geophys Res Lett 41(16):5904–5911.

Cattivelli, L., Di Fonzo, N., Mastrangelo, A. M., Mazzucco, L., Rascio, A. and Russo, M. (2000). Molecular aspects of abiotic stress resistance in durum wheat. In: Royo C, Nachit M, Di Fonzo N, Araus JL (eds) Durum wheat improvement in the Mediterranean region: new challenges. CIHEAM, Zaragoza, pp 207–213.

Cattivelli, L., Rizza, F., Badeck, F. W., Mazzucotelli, E., Mastrangelo, A. M., Francia, E., Mare, C., Tondelli, A. and Stanca, A. M. (2008). Drought tolerance improvement in crop plants: an integrated view from breeding to genomics. Field Crops Res. 105, 1–14. doi: 10.1016/j.fcr.2007.07.004.

Cechin, I., Cardoso, G. S., Fumis, T. F. and Corniani, N. (2015). Nitric oxide reduces oxidative damage induced by water stress in sunflower plants. Bragantia, Campinas, v. 74, no. 2, p200-206.

Cechin, I., Rossi, S. C., Oliveira, V. C. and Fumis, T. F. (2006). Photosynthetic responses and proline content of mature and young leaves of sunflower plants under water deficit. Photsynthetica, 44, 143-146.

Chai, H. H., Massawe, F. and Mayes, S. (2016). Effects of mild drought stress on the morpho-physiological characteristics of a bambara groundnut segregating population. Euphytica, 208:225–236. DOI 10.1007/s10681-015-1581-2.

Chakraborty, K., Bishi, S. K., Singh, A. L., Kalariya, K. A. and Kumar, L. (2013). Moisture deficit stress affects yield and quality in groundnut seeds. Indian Journal of Plant Physiology. p1-9. DOI 10.1007/s40502-013-0020-4.

Chakraborty, K., Singh, A. L., Kalariya, K. A., Goswami, N. and Zala, P. V. (2015). Physiological responses of peanut (*Arachis hypogaea* L.) cultivars to water deficit stress: status of oxidative stress and antioxidant enzyme activities. Acta Bot. Croat. 74 (1), 123–142. DOI: 10.1515/botcro-2015-0011.

Chattaraj, S., Chakraborty, D., Sehgal, V. K., Paul, R. K., Singh, S. D., Daripa, A. and Pathak, H., (2014). Predicting the impact of climate change on water requirement of wheat in the semi-arid Indo-Gangetic Plains of India. Agric. Ecosyst. Environ. 197, 174–183.

Chavarria, G. and Pessoa dos Santos, H. (2012). Plant Water Relations: Absorption, Transport and Control Mechanisms. Advances in Selected Plant Physiology Aspects. p106-132. DOI: 10.5772/33478.

Chaves, M. M. and Oliveira, M. M. (2004). Mechanisms underlying plant resilience to water deficits: prospects for water-saving agriculture. Journal of Experimental Botany, Vol. 55, No. 407, pp. 2365–2384, doi:10.1093.

Chaves, M. M., Maroco, J. P. and Pereira, J. S. (2003). Understanding plant responses to drought from genes to the whole plant: *Functional Plant Biology*. 30: 239-264.

Chen, H. and Jiang, J-G. (2010). Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. Environ Rev 18: 309–319.

Chen, S. T., Kuo, C. C. and Yu, P. S. (2009). Historical trends and variability of meteorological droughts in Taiwan. Hydrolog Sci J; 54: 430-441.

Chen, Y. L., Dunbabin, V. M., Diggle, A. J., Siddique, K. H. M. and Rengel, Z. (2012). Assessing variability in root traits of wild *Lupinus angustifolius* germplasm: basis for modelling root system structure. Plant and Soil 354, 141–155.

Chen, Y., Ghanem, M. E. and Siddique, K. H. M. (2016). Characterising root trait variability in chickpea (*Cicer arietinum* L.) germplasm. *Journal of Experimental Botany* doi:10.1093/jxb/erw368.

Chibarabada, T. P., Modi, A. T. and Mabhaudhi, T. (2015a). Water use characteristics of a bambara groundnut (*Vigna subterranea* L. Verdc) landrace during seedling establishment. Water SA, 41(4), 472–482. https://doi.org/10.4314/wsa.v41i4.06.

Chibarabada, T. P., Modi, A. T. and Mabhaudhi, T. (2015b). Bambara groundnut (Vigna subterranea) seed quality in response to water stress on maternal plants, Acta Agriculturae Scandinavica, Section B — Soil & Plant Science, 65:4, 364-373, DOI: 10.1080/09064710.2015.1013979.

Chibarabada, T. P., Modi, A. T. and Mabhaudhi, T. (2017). Expounding the Value of Grain Legumes in the Semi- and Arid Tropics. Sustainability, 9 (60); doi: 10.3390/su9010060.

Chimenti, C. A., Marcantonio, M. and Hall, A. J. (2006). Divergent selection for osmotic adjustment results in improved drought tolerance in maize (Zea mays L.) in both early growth and flowering phases. Field Crops Res. 95, 305–315.

Chinnusamy, V., Zhu, J. and Zhu, J. K. (2007). Cold stress regulation of gene expression in plants. Trends Plant Sci. 12, 444–451.

Chivenge, P., Mabhaudhi, Modi, A. T. and Mafongoya, P. (2015). The potential role of neglected and underutilized crop species as future crops under water scarce conditions in Sub-Saharan Africa. Int. J. Environ. Res. Public Health; 12:5685–5711.

Christopher, J., Christopher, M., Jennings, R., et al. (2013). QTL for root angle and number in a population developed from bread wheats (*Triticum aestivum*) with contrasting adaptation to water-limited environments. Theoretical and Applied Genetics 126, 1563–1574.

Cisse, L. and Amar, B. (2000). The importance of phosphatic fertilizer for increased crop production in developing countries. In Proceedings of the AFA 6th International Annual Conference, Cairo, Egypt.

Cleasby, P., Massawe, F. J. and Symonds, R. S. (2016). Bambara Groundnut for Food Security in the Changing African Climate. *Sustainable Agriculture Reviews, Vol 19,* pp 363-389.

Cleland, E., Chuine, I., Menzel, A., Mooney, H. and Schwartz, M. (2007). Shifting plant phenology in response to global change. Trends Ecol. Evol., 22, 357–365.

Cline, W. R. (2008). "Global Warming and Agriculture", Finance and Development (International Monetary Fund) 45 (1).

Cobb, J., DeClerck, G., Greenberg, A., Clark, R. and McCouch, S. (2013). Next-generation phenotyping: requirements and strategies for enhancing our understanding of genotype–phenotype relationships and its relevance to crop improvement. Theor Appl Genet. 126:867–87.

Collino, D. J., Dardanelli, J. L., Sereno, R. and Racca, R. W. (2001). Physiological responses of argentine peanut varieties to water stress. Light interception, radiation use efficiency and portioning assimilates. Field. Crops. Res, 70 (3): 177-184.

Collinson, S. T., Azam-Ali, S. N., Chavula, K. M. and Hodson, D. A. (1996). Growth, development and yield of Bambara groundnut (*Vigna subterranea*) in response to soil moisture. *The Journal of Agricultural Science* 126 (3), 307–318.

Collinson, S. T., Azam-Ali, S. N., Chavula, K. M. and Hodson, D. (1993). Growth, development and yield of bambara groundnut (*Vignasubterranea*) in response to soil moisture. Department Agriculture and Horticulture, University of Nottingham, Sutton Bonington Campus.Leics, LE12 5RD, UK.

Collinson, S. T., Berchie, J. and Azam-Ali, S. N. (1999). The effect of soil moisture on light interception and the conversion coefficient for three landraces of bambara groundnut (*Vigna subterranea*) J. of Agric. Science 133: 151-157.

Collinson, S. T., Clawson, E. J., Azam-Ali, S. N. and Black, C. R. (1997). Effect of soil moisture deficits on the water relations of Bambara groundnut (*Vigna subterranea* L. Verdc). Journal of Experimental Botany, 48, 877–884.

Collinson, S. T., Sibuga, K. P., Tarimo, A. J. P. and Azam-Ali, S. N. (2000). Influence of sowing date on the growth and yield of Bambara groundnut landraces in Tanzania. Experimental Agriculture, 36, 1–13.

Connor, D. J. and Sadras, V. O. (1992). Physiology of yield expression in sunflower. Field Crops Research, 30, 333-389.

Cornelissen, R. L. (2005). Modelling variation in the physiology of Bambara Groundnut (*Vigna subterranea* (L.) Verdc). PhD Thesis, Cranfield University. pp 170.

Cornic, G. (2000). Drought stress inhibits photosynthesis by decreasing stomatal aperture - not by affecting ATP synthesis. Trends Plant Sci., 5: 187-188.

Coupel-Ledru, A., Lebon, E ´., Christophe, A., Doligez, A., Cabrera-Bosquet, L., Pe´chier, P., et al. (2014). Genetic variation in a grapevine progeny (Vitis vinifera L. cvs Grenache x Syrah) reveals inconsistencies between maintenance of daytime leaf water potential and response of transpiration rate under drought. Journal of Experimental Botany, 65, 6205–6218.

Cowling, W. A., Li, L., Siddique, K. H. M., Henryon, M., Berg, P., Banks, R.G. and Kinghorn, B. P. (2017). Evolving gene banks: improving diverse populations of crop and exotic germplasm with optimal contribution selection. Journal of Experimental Botany 68, 1927–1939.

Cresswell, H. P. and Hamilton (2002). Particle Size Analysis. In: Soil Physical Measurement and Interpretation For Land Evaluation. (Eds. NJ McKenzie, HP Cresswell and KJ Coughlan) CSIRO Publishing: Collingwood, Victoria. pp 224-239.

CSIR. (2008). Biochemistry Division, CSIR-Crops Res. Institute. June 2008.

Cullis, C. and Kunert, K. J. (2017). Unlocking the potential of orphan legumes, *J. Exp. Bot.* 68, pp 1895–1903. 10.1093/jxb/erw437.

Da Costa, R. C. L., da Silva Lobato, A. K., da Silveira, J. A. G. and Laughinghouse, H. D. (2011). ABA-mediated proline synthesis in cowpea leaves exposed to water deficiency and rehydration. *Turkish Journal of Agriculture and Forestry* 35: 309–317.

Dai, A. (2011). "Drought under global warming: A review". Wiley Interdisciplinary Reviews: Climate Change 2: 45–65. doi:10.1002/wcc.81.

Dapaah, H. K., Mohammed, I. and Awuah, R. T. (2014). Phenological Development and Yield of Three Groundnut Varieties as Influenced by Plant Density in a Forest-savanna Transition Zone. International Journal of Agricultural Research, 9: 87-98. DOI: 10.3923/ijar.2014.87.98.

Daryanto, S., Wang, L. and Jacinthe, P. A. (2015). Global Synthesis of Drought Effects on Food Legume Production PLoS ONE. 10(6); 1-16.

Davies, W. J. and Zhang, J. (1991). Root signals and the regulation of growth and development of plants in drying soil. Annu. Rev. Plant Physiol. Plant Mol. Biol., 42: 55-76.

Davies, W. J., Tardieu, F. and Trejo, C. L. (1994). How do chemical signals work in plants that grow in drying soil? Plant Physiol., 104: 309-314.

Davis, B., Di Giuseppe, S. and Zezza, A. (2017). Are African Households (Not) leaving agriculture? Patterns of households' income sources in rural Sub-Saharan Africa Food Policy, 67 (2017), pp. 153-174.

de Faria., S. M., Lewis, G. P., Sprent, J. I. and Sutherland, J. M. (1989). Occurrence of nodulation in the leguminosae. New Phytol 111: 607 –619.

de Lima Pereira, J. W., Albuquerque, M. B., Filho, P. A. M., Nogueira, R. J. M. C., de Lima, L. M. and Santos, R. C. (2016). Assessment of drought tolerance of peanut cultivars based on physiological and yield traits in a semiarid environment. Agricultural Water Management. (166) p 70–76.

Deak, K. I. and Malamy, J. (2005). Osmotic regulation of root system architecture. *Plant J.*; 43(1): 17–28.

Del Blanco, I. A., Rajaram, S., Kronstad, W. E. and Reynolds, M. P. (2000). Physiological performance of synthetic hexaploid wheat–derived populations. *J. Crop Sci.* 40: 1257-1263.

Demirevska, K., Zasheva, D., Dimitrov, R., Simova-Stoilova, L., Stamenova, M. and Feller U. (2009). Drought stress effects on Rubisco in wheat: changes in the Rubisco large subunit. Acta Physiol. Plant. 31 1129–1138. 10.1007/s11738-009-0331-2.

Devries, J. D., Bennett, J. M., Albrecht, S. L. and Boote, K. J. (1989). Water relations, nitrogenase activity and root development of three grain legumes in response to soil water deficits. *Field Crops Research* 21, 215-226.

Ding, H., Zhang, Z. M., Dai, L. X., Kang, T., Ci, D. W. and Song, W. W. (2013).Effects of drought stress on the root growth and development and physiological characteristics of peanut. Ying Yong Sheng Tai Xue Bao. 24 (6):1586-92.

Ding, Y., Hayes, M. J. and Widhalm, M. (2011). "Measuring economic impacts of drought: A review and discussion". Disaster Prevention and Management **20** (4): 434. doi:10.1108/09653561111161752.

Doku, C., Sparks, A. H. and Zwart, S. J. (2016). Spatial modelling of rice yield losses in Tanzania due to bacterial leaf blight and leaf blast in a changing climate. Climatic Change. 135:569 - 583. doi: 10.1007/ s10584-015-1580-2. WOS: 000375466700015.

Doku, E. V. and Karikari, S. K. (1971). Fruit development in Bambara groundnut (*Voandzeia subterranean*). Annuals of Botany 34: 951-956.

Doungmanee, P. (2016). The nexus of agricultural water use and economic development level. Kasetsart Journal of Social Sciences 37; 38 – 45.

Echer, F. R. and Rosolem, C. A. (2015). Cotton leaf gas exchange responses to irradiance and leaf aging. Biologia Plantarum 59 (2): 366-372, 2015 DOI: 10.1007/s10535-015-0484-3.

Efeoglu, B., Ekmekci, Y. and Cicek, N. (2009). Physiological responses of three maize cultivars to drought stress and recovery. S. Afr. J. Bot., 75, 34–42.

Effa, E. B. and Uko, A. E. (2017), “Food security potentials of Bambara groundnut (Vigna subterranea (L.) Verdc)”, International Journal of Development and Sustainability, Vol. 6No. 12, pp.1919-1930.

eJournal, 10: 1-12.

Fageria, N. K., Baligar, V. C. and Clark, R. B. (2006). Physiology of crop production. Food Products Press. New York.

Fang, Y., Du, Y., Wang, J., Wu, A., Qiao, S., Xu, B., Zhang, S., Siddique, K. and Chen, Y. (2017). Moderate drought stress affected root growth and grain yield in old, modern and newly released cultivars of winter wheat. Front. Plant Sci. 8:672. doi:10.3389/fpls.2017.00672.

FAO (Food and Agriculture Organization). (2011a). Climate change, water and food security. Food and Agriculture Organization of United Nations. Rome, Italy, p200.

FAO (Food and Agriculture Organization). (2014a). The State of Food and Agriculture: Innovation in family farming. Rome, Italy. p23.

FAO (Food and Agriculture Organization). (2014b). FAOSTAT. Food and Agriculture Organization of the United Nations. Available at www.fao.org/faostat/en/. Accessed on 26 January 2019.

FAO (Food and Agriculture Organization). (2016c). Climate Change and Food Security: Risks and Responses. Food and Agriculture Organization of the United Nations. p110.

FAO (Food and Agriculture Organization). (2017a). The impact of disasters on agriculture. Food and Agriculture Organization of the United Nations. Rome, Italy. p28.

FAO (Food and Agriculture Organization). (2017b). The Future of food and agriculture: Trends and challenges. Food and Agriculture Organization of the United Nations, Rome, Italy. pp180.

FAO (Food and Agriculture Organization). (2017c). Tracking adaptation in agricultural sectors. Climate change adaptation indicators. Food and Agriculture Organization of the United Nations, Rome, Italy. p83.

FAO (Food and Agriculture Organization). (2018b). FAO's Work on Climate Change. United Nations Climate Change Conference 2018. p40.

FAO (Food and Agriculture Organization). (2018c). The State of Agricultural Commodity Markets 2018. Agricultural trade, climate change and food security. Rome, Italy. p112.

FAO. (1961). Agricultural and Horticultural Seeds. FAO Agricultural Studies No. 55, Food and Agricultural Organization, Rome, Italy.

FAO. (2004). The State of Agricultural Commodity Markets UN Food and Agriculture Organization; Rome: United Nations.

FAO. (2005). "Water Use in Agriculture" Food and Agricultural Organization. Retrieved: 8 April, 2016.

FAO. (2009). FAOSTAT Food and Agriculture Organization, Available online: http://faostat.fao.org/site/ 567/default.aspx#ancor (accessed on 17 December 2018).

FAO. (2013a). "Water Management: Towards 2030" .Retrieved: 8 April 2016.

FAO. (2013b). FAOSTAT. Database in crop production.[http:// faostat.fao.org/site/567/ DesktopDefau laspx?PageID=567#ancor] site visited on 5/08/2017.

FAO. (2016a). The state of food and agriculture: Climate change, agriculture and food security. Food and Agriculture Organization of United Nations, Rome Italy, p194.

FAO. (2016b). *AQUASTAT website*. Food and Agriculture Organization of the United Nations (FAO). Website accessed on [2018/12/26].

FAO. (2018a). The State of Food Security and Nutrition in the World. Building climate resilience for food security and nutrition. Rome, Italy.

Farkhutdinov, R. G., Teplova, I. R., Mitrichenko, A. N., Kudeyaro, V. A. and Veselov, S. Y. (2003). Effect of High Air Temperature on Cytokinins and Abscisic Acid Contents as Well as Water Balance in Wheat Seedlings. Biology Bulletin 30, 155-159.

Farooq, M., Basra, S. M. A., Wahid, A., Cheema, Z. A., Cheema, M. A. and Khaliq, A. (2008). Physiological role of exogenously applied glycinebetaine in improving drought tolerance of fine grain aromatic rice (*Oryza sativa* L.). *J. Agron. Crop Sci*. 194:325–333.

Farooq, M., Hussain, M., Wahid, A. and Siddique, K. H. M. (2012). Drought stress in plants: An overview. In Plant Responses to Drought Stress from Morphological to Molecular Features; Aroca, R., Ed.; Springer-Verlag: Berlin, Germany. pp. 1–36.

Farooq, M., Wahid, A., Kobayashi, N., Fujita, D. and Basra S. M. A. (2009). Plant drought stress: effects, mechanisms and management. Agronomy for Sustainable Development 29: 185-212.

Farrar, J. F. (1996). Sinks – integral parts of a whole plant. J. Exp.Bot.47, 1273–1279.

Fathi, A. and Tari, D. B. (2016). Effect of drought stress and its mechanism in plants. Int. J. Life Sci. 10, 1–6. Chakraborty, K., Singh, A. L., Kalariya, K. A., Goswami, N. and Zala, P. V. (2015). Physiological responses of peanut (*Arachis hypogaea* L.) cultivars to water deficit stress: status of oxidative stress and antioxidant enzyme activities. Acta Bot. Croat. 74 (1), 123–142.

Fenta, B. A., Beebe, S. E., Kunert, K. J. Burridge, J. D., Barlow, K. M., Lynch, J. P. and Foyer, C. H. (2014). Field Phenotyping of Soybean Roots for Drought Stress Tolerance. Agronomy, (4), 418-435; doi: 10.3390/agronomy4030418.

Fieldman, A., Kuan Ho, W., Massawe, F. and Mayes, S. (2019). Bambara Groundnut is a Climate-Resilient Crop: How Could a Drought-Tolerant and Nutritious Legume Improve Community Resilience in the Face of Climate Change?: Combating Climate Change by Adaptation. 10.1007/978-3-319-77878-5_8.

Filella, I., Serrano, L., Serra, J. and Peñuelas, J. (1995). Evaluating wheat nitrogen status with canopy reflectance indices and discriminant analysis. *Crop Science* 35, 1400–1405.

Fitter, A. (1996). Characteristics and functions of root systems. In *Plant Roots: The Hidden Half*, 2nd ed.; Waisel, Y., Eshel, A., Kafkafi, U., Eds.; Marcel Dekker: New York, NY, USA, pp. 1–20.

Fleissner, K. (2002). Management practices and preferences of bambara groundnut producers in Oshna region, north central Namibia. *In*: A. Sesay, O. T. Edje & R. Cornelissen, eds. *Increasing the productivity of bambara groundnut (Vigna subterranea) for sustainable food production in semi-arid Africa, Proceedings of a Mid-Project workshop*, University of Swaziland, Kwaluseni Campus, 47 – 53.

Flexas, J., Bota, J., Loreto, F., Cornic G. and Sharkey, T. D. (2004). Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. Plant Biol., 6: 1-11.

Foyer, C. H., Lam, H-M., Nguyen, H. T., Siddique, K. H. M., Varshney, R., Colmer, T. D., Cowling, W., Bramley, H., Mori, T. A., Hodgson, J. M., Cooper, J. W., Miller, A. J., Kunert, K., Vorster, J., Cullis, C., Ozga, J. A., Wahlqvist, M. L., Liang, Y., Shou, H., Shi, K., Yu, J.,

Fodor, N., Kaiser, B. N., Wong, F. L. and Valliyodan, B. (2016). Neglecting legumes has compromised global food and nutritional security. Nature Plants 2:16112. doi: 10.1038/nplants.2016.112.

Frechilla, S., Gonzalez, E. M., Royuela, M., Minchin, F. R., Aparicio-Tejo, P. M. and Arrese-Igor, C. (2000). Source of nitrogen nutrition (nitrogen fixation or nitrate assimilation) is a major factor involved in pea response to moderate water stress. Journal of Plant Physiology. 2000; 157:609–17.

Fu, J. and Huang, B. (2001). Involvement of antioxidants and lipid peroxidation in the adaptation of two cool season grasses to localized drought stress. *Environ. Exp. Bot*, 45:105-114.

Furbank, R. T. and Tester, M. (2011). Phenomics—Technologies to relieve the phenotyping bottleneck. *Trends Plant Sci.*, *16*, 635–644.

Garay, A. F. and Wilhelm, W.W. (1982). Root system characteristics of two soybean isolines undergoing water stress conditions. *Agron. J.*, *75*, 973–977.

Garcia-Mata, C. and Lamattina, L. (2009). Nitric Oxide Induces Stomatal Closure and Enhances the Adaptive Plant Responses against Drought Stress (vol 126, pg 1196, 2001). Plant Physiology 150: 531-531.

Garnett, T., Appleby, M. C., Balmford, A., Bateman, I. J., Benton, T. G. and Bloomer, P. et al., (2013). Sustainable intensification in agriculture: Premises and policies. *Science* 341:33–34.

Gautam, M. (2006). Managing Droughtin Sub Saharan Africa: policy perspectives. Invited Paper Prepared for a Panel Session on Drought: Economic Consequences and Policies

for Mitigation, at the IAAE Conference, Gold Coast, Queensland, Australia, August12–18, 2006.

Gholamin, R. and Khayatnezhad, M. (2011). The effect of end season drought stress on the chlorophyll content, chlorophyll fluorescence parameters and yield in maize cultivars. Sci. Res. Essay 6, 5351-5357.

Gibbon, D. and Pain, A. (1985). Crops of the Drier Regions of the Tropics, Longman Scientific and Technical Longman Group UK Ltd.

Gibon, Y., Ronan, S. and Larher, F. (2000). Proline accumulation in canola leaf discs subjected to osmotic stress is related to the loss of chlorophylls and to the decrease of mitochondrial activity. *Physiologia Plantarum,* 110: 469–476.

Gindaba, J., Rozanov, A. and Negash, L. (2004). Response of seedlings of two Eucalyptus and three deciduous tree species from Ethiopia to severe water stress. Forest Ecology and Management 201(1), 119–129.

Girdthai, T., Jogloy, S., Akkasaeng, C., Vorasoot, N., Wongkaew, S., Holbrook, C. C. et al. (2010). Heritability of, and genotypic correlations between, aflatoxin traits and physiological traits for drought tolerance under end of season drought in peanut (*Arachis hypogaea* L.) Field Crops Research 118:169-176. doi:10.1016/j.

Goli, A. E. (1995). Bibliographical Review. In: Begemann, F. and Mushonga, J.N., Eds., Proceedings of the Workshop on Conservation and Improvement of Bambara Groundnut (Vigna subterranean [L.] Verdc), International Plant Genetic Resources Institute, Harare, 4-10.

Gomes, F. P., Oliva, M. A., Mielke, M. S., Almeida, A. A. F. and Aquino, L. A. (2010). Osmotic adjustment, proline accumulation and cell membrane stability in leaves of *Cocos nucifera* submitted to drought stress. *Scientia Horticulturae* 126: 379–384.

Gowda, C. L. L., Pundir, R. P. S., Chaturvedi, S. K., Basu, P. S. and Singh, I. P. (2011). Phenotyping groundnuts for adaptation to drought. In: Drought phenotyping in crops: from theory to practice CGIAR. p238.

Gray, S. B. and Brady, S. M. (2016). Plant developmental responses to climate change. Developmental Biology 419; 64–77.

Guarino, L. and Lobell, D. B. (2011). A walk on the wild side. *Nature Climate Change* 1:374–375.

Guerrero, F. and Mullet, J. E. (1986). Increased abscisic acid biosynthesis during plant dehydration requires transcription. Plant Physiol., 80: 588-591.

Guo, J. M., Jermyn, W. A. and Turnbull, M. H. (2002). Diurnal and seasonal photosynthesis in two asparagus cultivars with contrasting yield. Crop Sci. 42:399-405.

Guo, P., Baum, M., Grando, S., Ceccarelli, S., Bai, G., Li, R., von Korff, M., Varshney, R. K., Graner, A. and Valkoun, J. (2009). Differentially expressed genes between drought-tolerant and drought-sensitive barley genotypes in response to drought stress during the reproductive stage. J. Exp. Bot., 60, 3531–3544.

Gupta, P. K., Balyan, H. S., Gahlaut, V. and Kulwal, P. L. (2012). Phenotyping, genetic dissection, and breeding for drought and heat tolerance in common wheat: Status and prospects. In Plant Breeding Reviews; Janick, J., Ed.; John Wiley and Sons: Hoboken, NJ, USA; pp. 85–168.

Hall, A. E. and Patel, P. N. (1985). Breeding for Resistance to Drought and Heat. In: Cowpea Research Production and Utilization, Singh, S.R. and K. O. Rachie (Eds.). Willey Publisher, New York, pp: 137-151.

Hamidou, F., Halilou, O. and Vadez, V. (2013). Assessment of Groundnut under Combined Heat and Drought Stress. *Journal of Agronomy and Crop Science*, *199*(1), 1–11.

Hamidou, F., Mariama, H., Achirou, F. B., Oumarou, H. and Vincent, V. (2018). Genotypic Variation for Root Development, Water Extraction and Yield Components in Groundnut under low Phosphorus and Drought Stresses. American Journal of Agriculture and Forestry; 6(5): 122-131.

Hamidou, F., Ratnakumar, P., Halilou, O., Mponda, O., Kapewa, T., Monyo, E., et al. (2012). Selection of intermittent drought tolerant lines across years and locations in the reference collection of groundnut (*Arachis hypogeae* L.). Field Crops Res. 126, 189–199. doi: 10.1016/j.fcr.2011.10.009.

Hannes, D., Eastwood, R. J. Guarino, L., Khoury, C. K., Müller, J. V. and Toll, J. (2014). Adapting Agriculture to Climate Change: A Global Initiative to Collect, Conserve, and Use Crop Wild Relatives, Agroecology and Sustainable Food Systems, 38:4, 369-377, DOI: 10.1080/21683565.2013.870629.

Hare, P. D., Cress, W. A. and Van Staden, J. (1998). Dissecting the roles of osmolyte accumulation during stress. Plant Cell Environ. 21:535–553.

Harris, D., Matthews, R. B., Nageswara Rao, R. C. and Williams, J. H. (1988). The physiological basis for yield difference between four genotypes of groundnut (*Arachis hypogaea* L.) in response to drought. Experimental Agriculture 24:215-226. doi:10.1017/S0014479700015969.

Harris, D., Tripathi, R. S. and Joshi, A. (2002). On-farm seed priming to improve crop establishment and yield in dry direct-seeded rice. In: Pandey, S., Mortimer, M., Wade, L., Tuong, T.P., Lopes, K., Hardy, B. (eds), *Direct seeding: Research Strategies and Opportunities*,Philippines: International Research Institute. pp 231-240.

Hasibeder, R., Fuchslueger, L., Richter A. and Bahn, M. (2014). Summer drought alters carbon allocation to roots and root respiration in mountain grassland. New Phytologist. 205: 1117–1127 doi: 10.1111/nph.13146.

Hassan, R. (2006). Climate change and African Agriculture. Policy no. 28. Assessing the impact of climate change on crop water use in South Africa, CEEPA Discussion paper no.28, CEEPA, University of Pretoria, pp 1-8.

Haworth, M., Killi, D., Materassi, A., Raschi, A. and Centritto, M. (2016). Impaired Stomatal Control is Associated with Reduced Photosynthetic Physiology in Crop Species Grown at Elevated [CO2]. Front. Plant Sci. 7:1568, p 1-13. doi: 10.3389/fpls.2016.01568.

Hayatu, M., Muhammad, S. Y. and Habibu, U. A. (2014). Effect of Water Stress on the Leaf Relative Water Content and Yield of some Cowpea (*Vigna Unguiculata* (L) Walp.) Genotype. International Journal of Scientific & Technology Research Volume 3, issue 7; 148 -15

Hellmuth, M. E., Moorhead, A., Thomson, M. C. and Williams, J. (Eds). (2007). Climate Risk Management in Africa: Learning from Practice. International Research Institute for Climate and Society (IRI), Columbia University, New York, USA.

Hepper, F. N. (1970). The bambara ground nut (*Voandzeia subterranea*). Field Crop Abstr. 23, 1-6.

Herridge, D. F., Peoples, M. B. and Boddey, R. M. (2008). Global inputs of biological nitrogen fixation in agricultural systems. Plant Soil; 311:1–18.

Heuer, B. (2010). Role of Proline in Plant Response to Drought and Salinity. Chapter In: Hand book of plant and crop stress. p 213 – 238. DOI: 10.1201/b10329-12.

Heuer, B. and Nadler, A. (1995). Growth, development and yield of potatoes under salinity and water deficit. *Australian J. Agric. Res*. 46: 1477–1486.

Hillocks, R. J., Bennett, C. and Mponda, O. M. (2012). Bambara nut: A review of utilisation, market potential and crop improvement. African Crop Science Journal. 20(*1*), 1–16.

HLPE. (2012). Food security and climate change. A report by the High Level Panel of Experts (HLPE) on Food Security and Nutrition of the Committee on World Food Security, Rome, Italy: Food and Agriculture Organization of the United Nations. (Accessed: 8 April 2016).

Ho, M. D., Rosas, J. C., Brown, K. M. and Lynch, J. P. (2005). Root architectural tradeoffs for water and phosphorus acquisition. Funct. Plant Biol. 32: 737-748.

Hoffmann, U. (2013). Agriculture a key driver and a major victim of global warming. Chapter 1, pp. 3, 5.

Hoshika, Y., Omasa, K. and Paoletti, E. (2013). Both ozone exposure and soil water stress are able to induce stomatal sluggishness. *Environ Exp Bot* 88: 19–23.

Hsiao, T. C. and Xu, L. K. (2000). Sensitivity of growth of roots versus leaves to water stress: Biophysical analysis and relation to water transport. *Journal of Experimental Botany* 51**:**1595-1616.

https://tjsgardendotcom1.wordpress.com/2015/09/10/what-is-drought-tolerant-pictures-of-drought-tolerant-plants/ (site visited on 16 November 2018).

https://weather-and-climate.com/average-monthly-precipitation-Rainfall,Mtwara,Tanzania. (site visited on 29 January 2019).

https://www.maximumyield.com/definition/327/days-to-maturity (Site visited on 20 June 2016).

https://www.weather.gov/media/owlie/2018_Drought.pdf (Site visited on 14 January 2019).

Huang, B. and Gao, H. (1999). Physiological responses of diverse tall fescue cultivars to drought stress. *Hort Sci*., 34: 897-901.

Huang, D., Wu, W., Abrams, S. R. and Cutler, A. J. (2008).The relationship of drought-related gene expression in *Arabidopsis thaliana* to hormonal and environmental factors. *J. Exp. Bot.* 59, 2991–3007.

Huber, S. C. and Huber, J. L. (1996). Role and regulation of sucrose phosphate synthase in higher plants. Ann Rev Plant Physiol Plant Mol Bio47:431–444.

Hund, A., Reimer, R. and Messmer, R. (2011). A consensus map of QTLs controlling the root length of maize. Plant Soil 344:143–158

Hussain, M., Malik, M. A., Farooq, M., Ashraf, M. Y. and Cheema, M. A. (2008). Improving drought tolerance by exogenous application of glycinebetaine and salicylic acid in sunflower. J. Agron. Crop Sci., 194: 193-199.

Ibraheem, A. S., Debbie, S. and Azam-Ali, S. (2014). Temperature and Drought Stress Effects on Growth and Development of Bambara Groundnut (Vigna Subterranea L.). Experimental Agriculture, 50(1):72–89.

Inuwa, R. S. and Muhammad, Y. Y. (2017). Drought Affects Protein and Phenolic Content in Bambara Groundnut (Vigna subterranea L. Verdc). Bayero Journal of Pure and Applied Sciences, 10(1): 345 – 34.

IPCC (Intergovernmental Panel on Climate Change). (2007). Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R. K and Reisinger, A. (Eds.)]. IPCC, Geneva, Switzerland, p104.

IPCC (Intergovernmental Panel on Climate Change). (2014). Climate change. Synthesis report. In: Core Writing Team, Pachauri R. K, Meyer L. A (eds). Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva 151 pp.

IPCC. (2013). Climate change: Climate change impacts, adaptation and vulnerability. Working group II contribution to AR5. http://www.ipcc-wg2.org/.

IPGRI. (2000). Descriptors for Bambara groundnut (*Vigna subterranea*). International Plant Genetic Resources Institute, Rome, Italy. p 57.

Iverson, C. M. (2014). Using root form to improve our understanding of root function. New Phytol., 203, 707–709.

Izanloo, A., Condon, A. G., Langridge, P., Tester, M. and Schnurbusch, T. (2008). Different mechanisms of adaptation to cyclic water stress in two South Australian bread wheat cultivars. J Exp Bot 59:3327–3346. doi:10.1093/jxb/ern199.

Jacqueline, W. L. P., Manoel, B. A., Pericles, A. M. F., Rejane, J. M. C. N., Liziane, M. L. and Roseane, C. S. (2016). Assessment of drought tolerance of peanut cultivars based on

physiological and yield traits in a semiarid environment. Agri. Water Management 166, 70–76.

Jaganathan, D., Thudi, M., Kale, S., Azam, S., Roorkiwal, M., Gaur, P. M., Kishor, P. B., Nguyen, H., Sutton, T. and Varshney, R. K. (2015). Genotyping-by-sequencing based intra-specific genetic map refines a 'QTL-hotspot' region for drought tolerance in chickpea. Molecular Genetics and Genomics 290, 559–571.

Jaimez, R. E., Vielma, O., Rada, F. and Garcia-Nunez, C. (2000). Effects of water deficit on the dynamics of flowering and fruit production in *Capsicum chinense* Jacq in a tropical semiarid region of Venezuela. J. Agron. Crop Sci., 185, 113-119.

Jaleel, C. A., Gopi, R., Sankar, B., Gomathinayagam, M. and Panneerselvam, R. (2008). Differential responses in water use efficiency in two varieties of *Catharanthus roseus* under drought stress. Comp. Rend. Biol., 331: 42-47.

Jaleel, C. A., Gopi, R., Sankar, B., Manivannan, P., Kishorekumar, A., Sridharan, R. and Panneerselvam, R. (2007) Studies on germination, seedling vigour, lipid peroxidation and proline metabolism in *Catharanthus roseus* seedlings under salt stress, South Afr. J. Bot. 73: 190–195.

James, R. F. (1990). Meteorology in America, 1800–1870. Baltimore, MD: Johns Hopkins University Press. ISBN 978-0801839580.

Janila, P., Nigam, S. N., Pandey, M. K., Nagesh, P. and Varshney, R. K. (2013). Groundnut improvement: use of genetic and genomic tools. Frontiers in Plant Science. 25; 4a23. doi:10.3389/fpls.2013.00023.

Jensen, E. S., Peoples, M. B. and Hauggaard-Nielsen, H. (2010). Faba bean in cropping systems. Field Crops Res. 115:203–216.

Jharna, D. E., Chowdhury, B. L. D., Haque, M. A., Bhuiyan, M. R. H. and Husain, M. M. (2001). Biochemical Screening of Some Groundnut (Arschis hypogaea L.) Genotypes for Drought Tolerance. Journal of Bilogical Science. 1(11): 1009 – 1011.

Jideani, V. A. and Diedericks, C. F. (2014). Nutritional, therapeutic, and prophylactic properties of Vigna subterranea and Moringa oleifera. In: Oguntibe, O. (Ed.), Antioxidant-antidiabetic Agents and Human Health. Janeza Trdine, 9, 51000 Rijeka, Croatia, pp. 187e201.

Jiwan, P. P. (2009). Leaf chlorophyll content. Journal of Remote Sensing Reviews Volume 5, pp 207-213.

Johnson, Y. K., Kinama, J. M., Ayuke, F. O. and Sijali, I. V. (2018). Determining the water use efficiency (WUE) of drought tolerant common bean varieties. Int. J. Agron. Agri. Res. 12(3), 35-45.

Jones, H. J. (1993). Drought tolerance and water-use efficiency. In: Smith J. A. C., Griffiths, H. (eds). Water deficits, plant response from cell to community. BIOS Scientific Publishers, Oxford, pp 193–203.

Jongrungklang, N., Toomsan, B., Vorasoot, N., Jogloy, S., Boote, K. J., Hoogenboom, G. T., and Patanothai, A. (2012). Classification of root distribution patterns and their contributions to yield in peanut genotypes under mid-season drought stress. Field Crops Res. 127, 181-190.

Jongrungklang, N., Toomsan, B., Vorasoot, N., Jogloy, S., Boote, K. J., Hoogenboom, G. T. and Patanothai, A. (2013). Drought tolerance mechanisms for yield responses to pre-flowering drought stress of diverse peanut genotypes. Field Crops Res. 144, 34-42.

Jorgensen, S. T., Liu, F., Ouedraogo, M., Ntundu, W. H., Sarrazin, J. and Christiansen, J. L. (2010). Drought responses of two bambara groundnut (Vigna subterranea L. Verdc) landraces collected from a dry and humid area of Africa. J. Agron. Crop Sci. 196 412–422.

Jorgensen, S. T., Ntundu, W. H., Ouedrago, M., Christiansen, J. L. and Liu, F. (2011). Effect of a short and severe intermittent drought on transpiration, seed yield, yield components, and harvest index in four landraces of Bambara groundnut. *International Journal of Plant Production* 5 (1), 1735–8045.

Judd, L. A., Jackson, B. E. and Fonteno, W. C. (2015). Advancements in Root Growth Measurement Technologies and Observation Capabilities for Container-Grown Plants. Plants 4, 369-392; doi: 10.3390/plants4030369.

Junjittakarn, J., Girdthai, T., Jogloy, S., Vorasoot, N. and Patanothai, A. (2014). Response of root characteristics and yield in peanut under terminal drought condition. Chil J Agric Res. 74:249-256.

Junjittakarn, J., Jogloy, S. Vorasoot, N. and Jongrungklang, N. (2016). Effect of mid-season drought and recovery on physiological traits and root system in peanut genotypes (*Arachis hypogaea* L.) SABRAO Journal of Breeding and Genetics 48 (3) 318-331.

Kabanda, T. (2018). Long-Term Rainfall Trends over the Tanzania Coast. Atmosphere. 9, (155); doi:10.3390/atmos9040155.

Kahane, R., Hodgkin, T., Jaenicke, H., Hoogendoorn, C., Hermann, M. et al., (2013). Agrobiodiversity for food security, health and income. Agronomy for Sustainable Development, Springer Verlag/EDP Sciences/INRA; 33 (4), pp.671-693.

Kakani, V. G., Prasad, P. V. V., Craufurd, P. Q. and Wheeler, T. R. (2002). Response of in vitro pollen germination and pollen tube growth of groundnut (*Arachis hypogaea L*.) genotypes to temperature. *Plant Cell and Environment* 25: 1651 – 1661.

Kalariya, K. A, Singh, A. L., Chakraborty, K., Zala, P. V. and Patel, C. B. (2013). Photosynthetic characteristics of groundnut (*Arachis hypogaea* L.) under water deficit stress. Indian J Plant Physiol 18(2):157–163.

Kamara, A. Y., Ekeleme, F., Kwari, J. D., Omoigui, L. O. and Chikoye, D. (2011). Phosphorus effect on growth and yield of groundnut varieties in the tropical savanna of North Eastern Nigeria. *Journal of Tropical Africa* 49(2): 24 – 30.

Kamble, P. N., Giri, S. P., Maneand, R. S. and Tiwana, A. (2015). Estimation of Chlorophyll Content in Young and Adult Leaves of Some Selected Plants. Universal Journal of Environmental Research and Technology Volume 5, Issue 6: 306-310.

Kanagaraj, P., Prince, K. S. J., Sheeba, J.A., Biji, K. R., Paul, S. B., Senthil, A. and Babu, R. C. (2010). Microsatellite markers linked to drought resistance in rice. *Curr. Sci.*, *98*, 836–839.

Karikari, S. K. Wigglesworth, D. J., Kwerepe, B. C., Balole, T. V., Sebolai, B. and Munthali, D. C. (1997). Botswana. *In*: J. Heller, F. Begemann & J. Mushonga, eds. *Proceedings of the workshop on conservation and improvement of bambara groundnut (Vigna subterranea (L) Verdc)*, Harare, Zimbabwe, 11 – 18.

Karikari, S. K., and Tabona, T. T. (2004). Constitutive traits and selective indices of Bambara groundnut (Vigna subterranea (L) Verdc) landraces for drought tolerance under Botswana conditions. Phys. Chem. Earth, 29: 1029-1034.

Karikari, S. K., Chaba, O. and Molosiwa, B. (1999). Effects of intercropping bambara groundnut on Pearl millet, Sorghum and Maize in Botswana. African Crop Science J., 7: 143-152.

Karim, T. D. A., Sanoussi, A., Maârouhi, I. M., Falalou, H. and Yacoubou, B. (2018). Effect of water deficit at different stages of development on the yield components of cowpea (*Vigna unguiculata* L. Walp) genotypes. African Journal of Biotechnology. Vol. 17(9), pp. 279-287.

Karunaratne, A. S., Azam Ali, S. N., Shareef, I., Sesay, A., Jorgensen, S. T. and Grout, N. M. J. (2010). Modelling the canopy development of bambara groundnut. *Agricultural and Forest Meteorology* 150: 1007-1015.

Karunaratne, A. S., Azam-Ali, S. N., Crout N. M. J., Mayes, S., Steduto, P. and Izzi, G. (2009). "Modelling the response of bambara groundnut: A key underutilized crop in agricultural systems". Proceedings of 23rd European Conference on Modelling and Simulation: ECMS, Madrid, Spain, 841-847.

Kashiwagi, J., Krishnamurthy, L., Crouch, J. H. and Serraj, R. (2006). Variability of root length density and its contributions to seed yield in chickpea (*Cicer arietinum* L.) under terminal drought stress. Field Crops Research 95,171–181.

Kashiwagi, J., Krishnamurthy, L., Purushothaman, R., Upadhyaya, H. D., Gaur, P. M., Gowda, C. L. L., Ito, O. and Varshney R. K. (2015). Scope for improvement of yield under drought through the root traits in chickpea (Cicer arietinum L.). Field Crops Research 170, 47–54.

Kashiwagi, J., Krishnamurthy, L., Upadhyaya, H. D., Krishna, H., Chandra, S., Vadez, V. and Serraj, R. (2005). Genetic variability of drought-avoidance root traits in the mini-core germplasm collection of chickpea (*Cicer arietinum* L.). Euphytica 146, p213–222.

Kato, Y., Abe, J., Kamoshita, A. and Yamagishi, J. (2006). Genotypic variation in root growth angle in rice (*Oryza sativa* L.) and its association with deep root development in upland fields with different water regimes. Plant and Soil 287, 117–129.

Kaur, G. and Asthir, B. (2015). Proline: a key player in plant abiotic stress tolerance. Biologia Plantarum 59 (4): 609-619.

Kavar, T., Maras, M., Kidric, M., Sustar-Vozlic, J. and Meglic, V. (2007). Identification of genes involved in the response of leaves of Phaseolus vulgaris to drought stress. *Mol.Breed*. 21, 81-87.

KaviKishor, P. B. and Sreenivasulu, N. (2014). Is proline accumulation per se correlated with stress tolerance or is proline homeostasis a more critical issue? Plant, Cell & Environment, 37, 300-311. http://dx.doi. org/10.1111/pce.12157. PMid: 23790054

Ketring, D. L. and Reid, J. L. (1993). Growth and peanut roots under field conditions. Agron. J. 85, 80–85.

Khayatnezhad, M., Gholamin, R., Jamaati-E Somarin, S., Zabihie-Kumar, R. R., Karajol, K. and Naik, G. R. (2011). Effect of polyethylene glycol induced water stress on physiological and biochemical responses in pigeonpea (*Cajanus cajan* L. Millsp.). *Recent Research in Science and Technology*. 3(1), 148-152.

Kiani, S. P., Maury, P., Sarrafi, A. and Grieu, P. (2008). QTL analysis of chlorophyll fluorescence parameters in sunflower (*Helianthus annuus* L.) under well watered and waterstressed conditions. *J. Plant Sci*. 175: 565–573.

Kilic, H., and, Yagbasanlar, T. (2010). The Effect of Drought Stress on Grain Yield, Yield Components and some Quality Traits of Durum Wheat (*Triticum turgidum* ssp. *durum*) Cultivars. Not. Bot. Hort. Agrobot. Cluj 38 (1), 164-170.

Kim, T. H., Bohmer, M., Hu, H. H., Nishimura, N. and Schroeder, J. I. (2010). Guard Cell Signal Transduction Network: Advances in Understanding Abscisic Acid, CO_2, and Ca^{2+}

Koolachart, R., Jogloy, S., Vorasoot, N., Wongkaew, S., Holbrook Jr, C. C., Jongrungklang, N., Kesmala, T. and Patanothai, A. (2013). Rooting traits of peanut genotypes with different yield responses to terminal drought. Field Crops Research. 149:366-378.

Kooyers, N. J. (2015). The evolution of drought escape and avoidance in natural herbaceous populations. Plant Sci. 234, 155–162. doi: 10.1016/j.

Krapovickas, A. and Gregory, W. C. (2007). Taxonomy of the genus Arachis (Leguminosae). Translated by D.E. Williams and C.E. Simpson. Bonplandia 16 (Supl.): 1-205. ISSN: 0524-0476.

Krishnamurthy, L., Johansen, C. and Ito, O. (1994). Genotypic variation in root system development and its implications for drought resistance in chickpea. In: Ito O, Johansen C, Adu-Gyamfi JJ, Katayama K, Kumar Rao JVDK, Rego TJ, eds. Roots and nitrogen in cropping systems of the semi-arid tropics. Proceedings of the international workshop: dynamics of the semi-arid tropics, ICRISAT. Patancheru, Andhra Pradesh, India, 21_ 25 November 1994, pp. 235_250.

Kumaga, F. K., Adiku, S. and Ofori, K. (2003). Effect of Post-flowering Water Stress on Dry Matter and Yield of Three Tropical Grain Legumes. International Journal of Agriculture & Biology; 5(4); pp 405–407.

Kumar, R. R., Karajol, K. and Naik, G. R. (2011). Effect of polyethylene glycol induced water stress on physiological and biochemical response in pigeonpea. *Plant Physiol*. 3:1487-152.

Lalk, I. and Doftling, K. (1985). Hardening, abscisic acid, proline and freezing resistance in two winter wheat varieties. Physiology Plantarum. 63:287-292.

Lambers, H., Chapin, F. S. and Pons, T. L. (2008). Plant Physiological Ecology. New York: Springer. ISBN 9780387783413.

Lanna, A. S., Mitsuzono, S.T., Terra, T. G. R., Vianello, R .P. and Carvalho, M. A. de F. (2016). Physiological characterization of common bean (*Phaseolus vulgaris* L.) genotypes, water-stress induced with contrasting response towards drought. Australian Journal of Crop Science; 10(1):1-6.

Lauriano, J. A., Ramalho, J. C., Lidon, F. C. and do Céu Matos, M. (2004). Peanut photosynthesis under drought and re-watering. Photosynthetica 42 (1): 37-41.

Lawson, T., Oxborough, K., Morison, J. I. L. and Baker, N. R. (2003). The responses of guard andmesophyll cell photosynthesis to CO2, O2, light and water stress in a range of species are similar. *J. Expl. Bot*. 54, 1743-1752.

Lee, D. K., Jung, H., Jang, G., Jeong, J. S., Kim, Y. S., Ha, S. H., Do-Choi, Y. and Kim, J. K. (2016). Overexpression of the OsERF71 transcription factor alters rice root structure and drought resistance. Plant Physiol. 172:575-588.

Leith, H. (1974). Phenology and Seasonality modeling Ecological Studies. Analysis and synthesis. Vol. 8. Springer Verlag. p 444.

Lemoine, R., Camera, S. L., Atanassova, R., De´dalde´champ, F., Allario, T., Pourtau, N., Bonnemain, J. L, Laloi, M., Coutos-The´venot, P., Maurousset, L., Faucher, M., Girousse, C., Lemonnier, P., Parrilla, J. and Durand, M. (2013). Source-to-sink transport of sugar and regulation by environmental factors. Front Plant Sci. doi:10. 3389/fpls.2013.00272.

Leung, K. and Bottomley, P. J. (1994). Influence of phosphate on the growth and nodulation characteristics of *Rhizobium trifolii*. *Applied and Environmental Microbiology*, 53, 2098-2105.

Levitt, E. (1980). “Chapter 4. Drought avoidance”, in Responses of Plants to Environmental Stresses, Vol. 2, ed. E. Levitt (New York, NY: Academic Press), 93–103.

Li, R., Guo, P., Baum, M., Grando, S. and Ceccarelli, S. (2006). Evaluation of chlorophyll content and fluorescence parameters as indicators of drought tolerance in barley. Agric. Sci. China, 5, 751–757.

Li, S. (2012). "Stressed Aquifers Around the Globe". New York Times. Retrieved 8 April, 2016.

Li, X. M., Zhang L. H., Ma L. J. and Li Y. Y. (2011). Elevated carbon dioxide and/or ozone concentrations induce hormonal changes in *Pinus tabulaeformis*. *J. Chem. Ecol.* 37 779–784.

Liang, X., Liu, Y., Chen, J. and Adams, C. (2017). Late-season photosynthetic rate and senescence were associated with grain yield in winter wheat of diverse origins. Journal of Agronomy and Crop Science, 204; 1 – 12.

Liang, X., Zhang, L., Natarajan, S. K. and Becker, D. F. (2013). Proline mechanisms of stress survival. Antioxidants & Redox Signaling 19: 998-1011.

Liang, Z. S., Yang, J. W., Shao, H. B. and Han, R. L. (2006). Investigation on water consumption characteristics and water use efficiency of poplar under soil water deficits on the Loess Plateau. Colloids Surf B Biointerfaces, 53:23-8.

Linnemann, A. R. (1987). Bambara groundnut (*Vigna subterranea* (L.) Verdc) – a review. *Abstracts on Tropical Agriculture*, 12(7), 9-16.

Linnemann, A. R. (1990). Cultivation of bambara groundnut *(Vigna subterranean* (L.) Verdc*)* in Western Province, Zambia.Report of a field study.TopicalCrops communication 15, 14pp.

Linnemann, A. R. and Azam-Ali, S. N. (1993). Bambara groundnut (Vigna subterranea (L.) Verdc) In: underutilized crops series 2. Vegetables and pulses (Editor: J. T.Williams). Chapman and Hall, London, UK, pp. 13 – 58.

Liu, F., Andersen, M. N. and Jensen, C.R. (2003). Loss of pot set caused by drought stress is associated with water status and ABA content of reproductive structures in soybean. Funct. Plant Biol. 30: 271-280.

Lobell, D. B., Bänziger, M., Magorokosho, C. and Vivek, B. (2011). Nonlinear heat effects on African maize as evidenced by historical yield trials. Nature Climate Change. 1, 42 -45.

Lodeiro, A. R., Gonzalez, P., Hernandez, A., Balague, L. J. and Favelukes, G. (2000). Comparison of drought tolerance in nitrogen-fixing and inorganic nitrogen-grown common beans. Plant Science. 154:31–41. PMID: 10725556.

Loladze, I. (2014). Hidden shift of the ionome of plants exposed to elevated CO2 depletes minerals at the base of human nutrition. *eLife* 3:e02245. doi: 10.7554/ eLife.02245.

Lopes, M. S., Araus, J. L., van Heerden, P. D. R. and Foyer, C. H. (2011). Enhancing drought tolerance in C4 crops. *J. Exp. Bot.*, *62*, 3135–3153.

Lowder, S. K., Skoet, J. and Raney, T. (2016). The Number, Size, and Distribution of Farms, Smallholder Farms, and Family Farms Worldwide World Development, vol. 87, issue C, 16-29.

Lu, Z. and Neumann, P. M. (1998). Water-stressed maize, barley, and rice seedlings show species diversity in mechanisms of leaf growth inhibition. J Exp Bot 49: 1945–1952.

Luan, S. (2002). Signalling drought in guard cells. Plant Cell and Environment 25: 229-237.

Ludi, E., Stevens, C., Peskett, L. and Cabral, L. (2007). Climate change and agriculture: Agricultural trade, markets and investment. Overseas Development Institute. pp 32.

Ludlow, M. M. (1989). Strategies of response to water stress. In: Kreeb KH,Richter H, Minckley TM, eds.Structural and functional responses to environmental stress. The Hague, the Netherlands: SPB Academic, 269–281.

Ludlow, M. M. and Muchow, R. C. (1990). A critical evaluation of traits for improving crop yields in water-limited environments. Adv Agron 43:107-153.

Ludlow, M.M. (1980). Adaptive significance of stomatal responses to water stress. In: *Adaptation of Plants to Water and High Temperature*, N.C. Turner and P.J. Kramer, eds. New York, Wiley.

Lugojan, C. and Ciulca, S. (2011). Evaluation of relative water content in winter wheat. J. Hortic. Fores. Biotechnol. 15: 173–177.

Lutts, S., Majerus, V. and Kinet, J. M. (1999). NaCl effects on proline metabolism in rice (Oryza sativa) seedlings. Physiologia Plantarum 105: 450–458.

Lynch, J. P. (2011). Root phenes for enhanced soil exploration and phosphorus acquisition: tools for future crops. Plant Physiol 156:1041–1049.

Lynch, J. P. (2013). Steep, cheap and deep: an ideotype to optimize water and N acquisition by maize root systems. Ann Bot 112:347–357.

Mabhaudhi, T. (2009). Responses of maize (Zea mays L.) landraces to water stress compared with commercial hybrids. M.Sc. Thesis. University of KwaZulu-Natal, Pietermaritzburg, South Africa.

Mabhaudhi, T. (2012). Drought Tolerance and Water–use of Selected South African Landraces of Taro (*Colocasia esculenta* l. Schott) and Bambara groundnut (*vigna subterranea* l. Verdc). PhD Thesis, University of KwaZulu-Natal Pietermaritzburg South Africa, p241.

Mabhaudhi, T. and Modi, A. T. (2011). Can hydro-priming improve germination vigour, speed and emergence of maize landraces under water stress? *J. Agric. Sci. Technol. B* 1 20–28.

Mabhaudhi, T. and Modi, A. T. (2013). Growth, phenological and yield responses of a bambara groundnut (Vigna subterranea L. Verdc) landrace to imposed water stress under field conditions. South African Journal of Plant and Soil; 30: 69-79.

Mabhaudhi, T. and Modi, A. T. (2015). Drought tolerance of selected South African taro (Colocasia esculenta L. Schott) Landraces. Experimental Agriculture 51:451-466.

Mabhaudhi, T., Chibarabada, T. and Modi A. (2016). Water-food-nutrition-health nexus: linking water to improving food, nutrition, and health in sub-Saharan Africa. Int. J. Environ. Res. Publ. Health 13, 107.

Mabhaudhi, T., Chibarabada, T. P., Chimonyo, V. G. P. and Modi, A. T. (2018). Modelling climate change impact: A case of bambara groundnut (*Vigna subterranea* L. Verdc). Modi Physics and Chemistry of the Earth. pp 1-8.

Mabhaudhi, T., Modi A. T., and Beletse, Y. G. (2013). Growth, phenological and yield responses of a bambara groundnut (Vigna subterranea L. Verdc) landrace to imposed water stress: ll. Rain shelter conditions. Water SA 39: 191-198.

Mace, E. S., Singh, V., Van Oosterom, E. J., Hammer, G. L., Hunt, C. H. and Jordan, D. R. (2012). QTL for nodal root angle in sorghum (*Sorghum bicolor* L. Moench) co-locate with QTL for traits associated with drought adaptation. Theoretical and Applied Genetics 124, 97–109.

Madhan, M. M. and Nigam, S. N. (2013). Principles and Practices for Groundnut Seed Production in India. Information Bulletin No. 94. International Crops Research Institute for the Semi-Arid Tropics, Andhra Pradesh, India. p64.

Madhusudhan, K. V. and Sudhakar, C. (2014b). Morphological responses of a high yielding groundnut cultivar (Arachis hypogaea L. cv. K-134) under water stress. Indian Journal of Pharmaceutical and Biological Research 2: 35-38.

Madhusudhan, K. V. and Sudhakar, C. (2014b). Morphological responses of a high yielding groundnut cultivar (Arachis hypogaea L. cv. K-134) under water stress. Indian Journal of Pharmaceutical and Biological Research 2: 35-38.

Madhusudhan, K. V., Giridarakumar, S., Ranganayakulu, G. S., Chandraobulreddy, P. and Sudhakar, C. (2002). Effect of water stress on some physiological responses in two groundnut (*Arachis hypogaea* L.) cultivars with contrasting drought tolerance. Journal of Plant Biology 29:199-202.

Madukwe D. K., Onuh, M. O. and Christo, I. E. C. (2011). Agronomic and Physiological Performance of Bambara Groundnut (*Vigna subterranea* (L.) Verdc) in Southeastern Nigeria. World Journal of Agricultural Sciences 7 (2): 166-171. ISSN 1817-3047.

Mafakheri, A., Siosemardeh, A. F., Bahramnejad, B., Struik, P. C. and Sohrabi, Y. (2010). Effect of drought stress on yield, proline and chlorophyll contents in three chickpea cultivars. Australia Journal of Crop Science, 4(8):580-585.

Mamadou, C. A., Ntare, B., Gracen, V. Danquah, E. Y. and Ofori, K. (2016). Evaluation of Groundnut Mini Core to Identify Sources of Tolerance to End of Season Drought in the Sahel, Niger. International Journal of Plant Breeding and Genetics ISSN 1819-3595 DOI: 10.3923/ijpbg.2017.31.38.

Manavalan, L. P., Guttikonda, S. K., Nguyen, V. T., Shannon, J. G. and Nguyen, H. T. (2010). Evaluation of diverse soybean germplasm for root growth and architecture. Plant Soil, 330, 503–514.

Manavalan, L. P., Guttikonda, S. K., Phan Tran, L. S. and Nguyen, H. T. (2009). Physiological and molecular approaches to improve drought resistance in soybean. *Plant Cell Physiol.*, *50*, 1260–1276.

Mangasini, A. K., Mwanahawa, L. M., Arbogast, G. and Neema, P. (2013). Socioeconomic factors limiting smallholder groundnut production in Tabora Region. [http.//:www.repoa.or.tz] site visited on 20/07/2015.

Manivannan, P., Jaleel, C.A., Sankar, B., Kishorekumar, A., Somasundaram, R., Alagu Lakshmanan, G. M. and Panneerselvam, R. (2007). Growth, biochemical modifications and proline metabolism in *Helianthus annuus* L. as induced by drought stress. *J. Colloids Surf. B: Biointerf*. 59: 141-149.

Manthe, C. S., Ramolemana, G., karikari, S. K., Khonga, E. B., Munthali, D. C. and Mothlanka, D. (2002). Preliminary survey of farmers' perceptions of Bambara groundnut (Vigna subterranea (L) VERDC) ideotype in Botswana. *In*: A. Sesay, O. T. Edje & R. Cornelissen, eds. *Increasing the productivity of bambara groundnut (Vigna subterranea) for sustainable food production in semi-arid Africa, Proceedings of a mid- Project workshop*, University of Swaziland, Kwaluseni, Campus, 39 – 45.

Marotzke, J. and Forster, P. M. (2015). Forcing, feedback and internal variability in global temperature trends. *Nature* 517, 565–570.

Márquez-García, B., Shaw, D., Cooper, J. W., Karpinska, B., Quain, M. D.,Makgopa, E. M., et al. (2015). Redox markers for drought-induced nodulesenescence, a process occurring after drought-induced senescence of the owest leaves in soybean (Glycine maxMerr.).Annals Bot.116, 497–510. doi:10.1093/aob/mcv030.

Martnez-Fernndez, J., Gonzlez-Zamora, A., Snchez, N. and Gumuzzio, A. (2015). A soilwater based index as a suitable agricultural drought indicator. J. Hydrol. 522,265–273.

Massawe, F. J., Dickinson, M., Roberts, J. A. and Azam-Ali, S. N. (2002). Genetic diversity in bambara groundnut landraces (*Vigna subterranea* (L.) Verdc) revealed by AFLP markers. *Genome* 45: 1175-1180.

Massawe, F. J., Mayes, S. and Cheng, A. (2016). Crop Diversity: An Unexploited Treasure Trove for Food Security Trends in Plant Science, Vol. 21, No. 5; 365 – 368.

Massawe, F. J., Mayes, S., Cheng, A., Chai, H. H., Cleasby, P., Symonds, R., Ho, W. K., Siise, A., Wong, Q. N. and Kendabie, P. (2015). The potential for underutilised crops to improve food security in the face of climate change. Procedia Environ. Sci. 29, 140–141.

Massawe, F. J., Mwale, S. S., Azam-Ali, S. N. and Roberts, J. (2005). "Breeding in Bambara Groundnut (*Vigna subterranea* (L.) Verdc): Strategic Considerations," *African Journal of Biotechnology*, Vol. 4, No. pp. 463-471.

Massawe, F. J., Mwale, S. S., Azam-Ali, S. N. and Roberts, J. A. (2007). Towards genetic improvement of bambara groundnut [*Vigna subterranea* (L.) Verdc]. In: Ochatt S, Jain SM (eds) Breeding of neglected and under-utilized crops: spices and herbs. Science Publishers, p 468.

Massawe, F., Schenkel, W. and Temba, E. M. (2003). Artificial hybridisation in bambara groundnut (Vigna subterranea (L.) Verdc). Proceedings of the International Bambara Groundnut Symposium, Botswana College of Agriculture. Botswana. Volume 1, p193 – 209.

Masset, G., Soler, L. G., Vieux, F. and Darmon, N. (2014) Identifying sustainablefoods: the relationship between environmental impact, nutritionalquality, and prices of foods representative of the french diet. JAcad Nutr Diet 114:862–869.

Mathoboa, R., Marais, D. and Steyna, J. M. (2017). The effect of drought stress on yield, leaf gaseous exchange and chlorophyll fluorescence of dry beans (Phaseolus vulgaris L.). Agricultural Water Management. p118 – 125.

Matsui, T. and Singh, B. B. (2003). Root characteristics in cowpea related to drought tolerance at the seedling stage. Experimental Agriculture 39:29-38 DOI 10.1017/S0014479703001108.

Mauromicale, G., Lerna, A. and Marchese, M. (2006). Chlorophyll fluorescence and chlorophyll content in field-grown potato as affected by nitrogen supply, genotype, and plant age. *Photosynthetica* 44: 76–82.

Mayes, S., Ho, W .K., Chai, H. H., Gao, X., Kundy, A, C., Mateva, K. I., Zahrulakmal, M., Hahiree, M. K. I. M., Kendabie, P., Licea, L. C. S., Massawe, F., Mabhaudhi, T., Modi, A. T. Berchie, J. N., Amoah, S., Faloye, B., Abberton, M., Olaniyi, O. and Azam-Ali, S. N. (Submitted). Bambara groundnut – an exemplar underutilised legume for resilience under climate change. Planta.

Mazahib, A., Nuha, M., Salawa, I. and Babiker, E. (2013). Some nutritional attributes of bambara groundnut as influenced by domestic processing. International Food Research Journal. 20; 1165 – 1171.

McKevith, B. (2004). Nutritional aspects of triticale. British Nutrition Foundation. *Nutr. Bull*., 29, 111–142.

Meena, S. L. and Massawe, F. J. (2013). Evaluation of Bambara groundnut (*Vigna subterranea*) landraces for their agronomic and physiological traits. *Indian Journal of Agricultural Sciences* 83 (5): 579–81.

Mehran, A., AghaKouchak, A., Nakhjiri, N., Stewardson, M. J., Peel, M. C., Phillips, T. J. Wada, Y. and Ravalico, J. K. (2017). Compounding Impacts of Human-Induced Water Stress and Climate Change on Water Availability. Scientific Reports. Volume 7, Article number: 6282. DOI:10.1038/s41598-017-06765.

Meister, R., Rajani, M. S., Ruzicka, D. and Schachtman, D. P. (2014). Challenges of modifying root traits in crops for agriculture. Trends in Plant Science 19, 779–788.

Mensah, J. K., B. O. Obadoni, P. G. Eruotor and Onome-Irieguna, F. (2006). Simulated flooding and drought effects on germination, growth and yield parameters of sesame (*Sesamum indicum* L.). Afr. J. Biotechnol., 5: 1249-1253.

Merzlyak, M. N., Gitelson, A. A., Chivkunova, O. B. and Rakitin, V. Y. (1999). Non-destructive optical detection of pigment changes during leaf senescence and fruit ripening. Physiologia Plantarum, 106, 135– 141.

Ming, Z., Li-feng, E., Kun, Z., Feng-zhen, L. and Yong-shan, W. (2017). Drought-induced responses of organic osmolytes and proline metabolism during pre-flowering stage in leaves of peanut (*Arachis hypogaea* L.). Author links open overlay panel. Journal of Integrative Agriculture, Volume 16, Issue 10, p 2197-2205.

Mirza, H., Kamrun, N., Md. Mahabub, A., Roychowdhury, R. and Fujita, M. (2013). Physiological, Biochemical, and Molecular Mechanisms of Heat Stress Tolerance in Plants. Int. J. Mol. Sci., 14, 9643-9684.

Mishra, A. K. and Singh, V. P. (2011). "Drought modelling – A review". Journal of Hydrology 403: 157. doi:10.1016/j.jhydrol.2011.03.049.

Mkandawire, C. H. (2007). Review of bambara groundnut production in sub-Saharan Africa. Agricultural Journal 2: 464– 70.

Moa, F., Zhanga, J., Wanga, J., Zheng-Guo, C., Guo-Jun, S., Hong-Xu, R., Xu-Zhe, Z., Cheruiyota, W. K., Kavagic, L., Jian-Yong, W. and You-Cai, X. (2017). Phenological evidence from China to address rapid shifts in global flowering times with recent climate change. Agricultural and Forest Meteorology 246; 22–30.

Mohamed, B. A., van Duivenbooden, N. and Abdoussallam, S. (2002). Impact of Climate Change on Agricultural Production in the Sahel Part 1. Methodological Approach and

Case Study for Millet in Niger. Climatic Change. 54:327 - 348. https://doi.org/10.1023/a:1016189605188.

Mohammadkhani, N. and Heidari, R. (2008). Drought-induced accumulation of soluble sugar and proline in two maize varieties. World Appl Sci J 3:448–453.

Mohammed, M. S. (2014). Pre-breeding of Bambara Groundnut (*Vigna subterranea* [L.] Verdc). PhD Thesis. University of KwaZulu-Natal, South Africa. p202.

Molden, D. (Ed.) (2007). "Findings of the Comprehensive Assessment of Water Management in Agriculture" Annual Report 2006/2007. International Water Management Institute. (Accesssed: 8 November 2016).

Molosiwa, O., Aliyu, S., Stadler, F., Mayes, K., Massawe, F. J., Kilian, A. and Mayes, S. (2015). SSR marker development, genetic diversity and population structure analysis of Bambara groundnut [Vigna subterranea (L.) Verdc] landraces. Genet Resour Crop Evol 62:1225–1243.

Monakhova, O. F. and Chernyadev, I. I. (2002). Protective Role of Kartolin-4 in Wheat Plants Exposed to Soil Drought. *Appl. Bioch. Micro*. 38:378-380.

Monneveux, P., Ribaut, Jean-M. and Okono, A. (Eds). (2014). Drought Phenotyping in Crops: From theory to practice. Frontiers in Physiology. p238.

Morgan, J. M. (1984). Osmoregulation and Water Stress in Higher Plants. Annu Rev Plant Physiol. 35: 299 - 319.

Morris, L. A. and Lowery, R. F. (1988). Influence of site preparation on soil conditions affecting stand establishment and tree growth. South. J. Appl. For.12 (3): 170-178.

Mowo, J. G., Floor, J., Kaihura, F. B. S. and Magoggo, J. P. (1993). Review of fertilizer recommendations in Tanzania. Soil Fertilty Report No. F6. p67.

Muhammad, Y. Y. (2014). Exploring the potential of Bambara groundnut, an underutilised African legume species, towards food security in Africa. African Journal of Agricultural Science and Technology; Vol. 2(11), pp. 201-204.

Muhammad, Y. Y. and Massawe, F. J. (2015). Photosynthetic gas exchange and chlorophyll in bambara groundnut (vigna subterranea l. Verdc) Subjected to water deficit. Bayero Journal of Pure and Applied Sciences, 8(1): 50 – 55.

Muhammad, Y. Y., Mayes, S., and Massawe, F. (2015). Effects of short-term water deficit stress on physiological characteristics of Bambara groundnut (Vigna subterranea (L.) Verdc). South African Journal of Plant and Soil, p 1 - 10. http://dx.doi.org/10.1080/02571862.2015.1056847.

Mungate, D. (1995). Opening address. Introduction. In: Heller, J., Begemann and Mushonga, J. (Eds). *Proceedings of the workshop on conservation and improvement of Bambara groundnut (Vigna subterranea (*L*.) Verdc), 14-16 November, Harare Zimbabwe*. pp 1

Munns, D. N and Fox, R. L. (1977). Comparative lime requirements of tropical and temperate legumes. *J. Plant and Soil* 46: 533- 548.

Munns, R. and King, R. W. (1988). Abscisic acid is not the only stomatal inhibitor in the transpiration stream of wheat plants. Plant Physiol., 88: 703-708.

Murevanhema, Y. Y. and Jideani, V. A. (2013). Potential of bambara groundnut (*Vigna subterranea* (L.) Verdc) milk as a probiotic beverage-a review. Crit Rev Food Sci Nut.; 53(9): 954–967.

Murillo-Amador, B., Ávila-Serrano, N. Y., García-Hernández, J. L., López-Aguilar, R., Troyo-Diéguez, E. and Kaya, C. (2004). Relationship between a nondestructive and an extraction method for measuring chlorophyll contents in cowpea leaves. *Journal of Plant Nutrition and Soil Science* 167, 363–364.

Mwale, S. S. (2005). Resource use efficiency of bambara groundnut landraces in response to soil water. PhD thesis. University of Nottingham.

Mwale, S. S., Azam-Ali, S. N. and Massawe, F. J. (2007a). Growth and development of bambara groundnut (*Vigna subterranea*) in response to soil moisture 1. Dry matter and yield. *European Journal of Agronomy* 26, 345-353.

Nageswara Rao, R. C. and Wright, G. C. (1994). Stability of the relationship between specific leaf area and carbon isotope discrimination across environments in peanut. Crop Sci., 34: 98-103.

Nageswara Rao, R. C., Sardar, S., Sivakumar, M. V. K., Srivastava, K. L. and Williams, J. H. (1985) Effect of water deficit at different growth phases of peanut. I. Yield responses. Agron J 77:782–786.

Nageswara Rao, R. C., Williams, J. H., Sikavumar, M. K. V. and Wadia, K. D. R. (1988). Effect of water deficit at different growth phases of peanut. II. Response to drought during preflowering phase, Agron. J. 80, 431–438.

Nah, S. and Chau, C. (2010). Issues and challenges in defeating world hunger. Trends in Food Science and Technology 21: 544-557.

Nam, N. H., Subbaroa, G. V., Chauhan, Y. S. and Johansen, C. (1998). Importance of canopy attributes in determining dry matter accumulation of pigeon pea under contrasting moisture regimes. Crop Sci., 38: 955-961.

Nanganoa, L. T., Okolle, J. N., Missi, V., Tueche, J. R., Levai, L. D., Njukeng, J. N. (2019) Impact of Different Land-Use Systems on Soil Physicochemical. Properties and Macrofauna Abundance in the Humid Tropics of Cameroon. Applied and Environmental Soil Science, 1-10.

Narayanan, S., Mohan, A., Gill, K. S. and Prasad, P. V. V. (2014). Variability of root traits in spring wheat germplasm. PLoS; 9, 0100317.

Nardini, A., Salleo, S. and Jansen, S. (2011). More than just a vulnerable pipeline: xylem physiology in the light of ion-mediated regulation of plant water transport. Journal of Experimental Botany, Vol. 62, No. 14, pp. 4701–4718, 2011doi:10.1093/jxb/err208.

Nardini, A., Salleo, S. and Tyree, M. T. (2002). Ecological aspects of water permeability in roots. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half. Marcel Dekker, New York, pp 683-698.

NARI (Naliendele Agricultural Research Institute). (2013). Annual oil seeds and legume crops research report 2012/13. Naliendele Agricultural Research Institute Annual Reports, p 110.

National Research Council. (1996). “Lost Crops of Africa: Vegetables,” National Academies Press, Washington DC, Vol. 2.

Naumann, G., Alfieri, L., Wyser, K., Mentaschi, L., Betts, R. A., Carrao, H., Spinoni, J., Vogt, J., and Feyen, L. (2018). Global changes in drought conditions under different levels of warming. *Geophysical Research Letters*, *45*, 3285–3296.

Nautiyal, P. C., Kulkarni, G., Singh, A. L. and Basu, M. S. (2017). Evaluation of water-deficit stress tolerance in Bambara groundnut landraces for cultivation in sub-tropical environments in India. Indian Journal of Plant Physiology. p8. DOI 10.1007/s40502-017-0296-x.

Nautiyal, P. C., Nageswara, R. C. and Joshi, Y. C. (2002). Moisture deficit induced changes in leaf water content, leaf carbon exchange rate and biomass production in groundnut cultivars differing in specific leaf area. Field Crop Research, 74, 67–79.

Nautiyal, P. C., Zala, P. V., Tomar, R. S., Sodavadiya, P. and Tavethia, B. (2011). Evaluation of water use efficient newly developed varieties of groundnut in on-farm trials in two different rainfall areas in Gujarat, India. *Journal of Agricultural Research* 9: 44 – 62.

Naylor, R. L., Falcon, W. P., Goodman, R. M., Jahn, M. M., Sengooba, T., Tefera, H., and Nelson, R. J. (2004). Biotechnology in the developing world: a case for increased investments in orphan crops. Food Policy 29, 15–44. doi: 10.1016/j. foodpol.2004.01.002.

Nemhauser, J. L., Hong, F. and Chory, J. (2006). Different plant hormones regulate similar processes through largely nonoverlapping transcriptional responses. *Cell* 126, 467–475.

Neto, A. D. A., Nogueira, R. J. M. C., Filho, P. A. M. and Santos, R. C. (2010). Physiological and biochemical responses of peanut genotypes to water deficit, Journal of Plant Interactions, 5:1, 1-10, DOI: 10.1080/17429140902999243.

Nielsen, K. L., Lynch, J.P. and Weiss, H. N. (1997). Fractal geometry of bean root systems: Correlations between spatial and fractal dimension. *Am. J. Bot.*, *84*, 26–33.

Nigam, S. N., Upadhayaya, H. D., Chandra, S., NageswaraRao, R. C., Wright, G. C. and Reddy, A. G. S. (2001). Gene effects for specific area and harvest index in three crosses of groundnut (*Arachis hypogaea L*.). *Annals of Applied Biology* 39(3): 301 – 306.

Nonami, H. (1998). Plant water relations and control of cell elongation at low water potentials. J. Plant Res., 111: 373-382.

Ntundu, W. H. (1997). Tanzania. *In*: J. Heller, F. Begemann and J. Mushonga, eds. *Proceedings of the workshop on conservation and improvement of bambara groundnut (Vigna subterranea (L)* Verdc*)*, Harare, Zimbabwe, 53-58.

Ntundu, W. H., Shillah, S. A., Marandu, W. Y. F., Christiansen, J. L., (2006). Morphological diversity of bambara groundnut (*Vigna subterranea* L. Verdc) landraces in Tanzania. Genet. Resour. Crop Evol. 53: 367-378.

Nuer, D. G. (1989). Light interception and dry matter production of bambara groundnut (Vigna subterranea) and groundnut (Arachis hypogaea) under irrigated and droughted conditions. M.Sc. University of Nottingham.

Ocran, V. K., Delimini, L. L., Asuboah, R. A and Asiedu, E. A. (1998). Seed Management Manual for Ghana, MOFA, Accra Ghana.

OECD (Organization for Economic Cooperation and Development). (2015). Agriculture and Climate Change. Trade and Agriculture Directorate. p6.

OECD/FAO. (2018). OECD-FAO Agricultural Outlook 2018-2027, OECD Publishing, Paris/Food and Agriculture Organization of the United Nations, Rome, Italy. p112.

Omoikhoje, S. O. (2008). Assessment of the nutritive value of bambara groundnut as influenced by cooking time. *Livestock Research for Rural Development. Volume 20,*

Article no.55. Retrieved April 14, 2016, from http://www.lrrd.org/lrrd20/4/omoi20055.htm

Osakabe, Y., Osakabe K., Shinozaki, K. and Tran, L.-S. P. (2014). Response of plants to water stress. *Front. Plant Sci.* 5:86. 10.3389/fpls.2014.00086.

Osmont, K. S., Sibout, R. and Hardtke, C. S. (2007). Hidden branches: Developments in root system architecture. *Annu. Rev. Plant Biol.*, *58*, 93–113.

Outlaw, W. H. (2003). Integration of cellular and physiological functions of guard cells. Critical Reviews in Plant Sciences 22: 503-529.

Oyelade, O. A., Ademiluyi, Y. S., James, D. and Ozumba, I. C. (2011). Performance Evaluation of a Modified Tractor Drawn Groundnut Digger/Shaker for Agricultural Productivity. "*tillage for Agriculture Productivity and Environmental Sustainability" Conference*. February 21-23. Ilorin, Nigeria. p191.

Oyeyinka, S. A., Singh, S., Adebola, P. O., Gerrano, A. S. and Amonsou, E. O. (2015). Physicochemical properties of starches with variable amylose contents extracted from bambara groundnut genotypes. *Carbohydr. Polym*. 133, 171–178.

Pace, J., Lee, N., Naik, H. S., Ganapathysubramanian, B. and Lübberstedt, T. (2014). Analysis of maize (*Zea mays* L.) seedling roots with the high-throughput image analysis tool *ARIA* (automatic root image analysis). *PLoS ONE*, doi:10.1371/journal.pone.0108255.

Padmavaghi, T. A. V. and Rao, D. M. (2013). Differential accumulation of osmolytes in four cultivars of peanut (*Arachis hypogaea* L.) under drought stress. Journal of Crop Science and Biotechnology 16: 151–159.

Padulosi, S., Bhag Mal, Bala Ravi, S., Gowda, J., Gowda, K. T. K., Shanthakumar, G., Yenagi, N. and Dutta, M. (2009). Food security and climate change: Role of plant genetic resources of minor millets. *Indian Journal of Plant Genetic Resources* 22(1): 1-16.

Paez-Garcia, A., Motes, C. M., Wolf-Rüdiger S., Chen, R., Blancaflor, E. B. and Monteros, M. J. (2015). Root Traits and Phenotyping Strategies for Plant Improvement. *Plants*, *4*, 334-355.

Painawadee, M., Jogloy, S., Kesmala, T., Akkasaeng, C. and Patanothai, A. (2009). Identification of traits related to drought resistance in peanut (Arachis hypogaea L.). Asian Journal of Plant Sciences 8(2); 120 -128.

Pandey, V. and Shukla, A. (2015). Acclimation and tolerance strategies of rice under drought stress. *Rice Sci.* 22, 147–161.doi:10.1016/j.rsci.2015.04.001

Pang, J., Turner, N. C., Du, Y-L., Colmer, T. D. and Siddique, K. H. M. (2017). Pattern of Water Use and Seed Yield under Terminal Drought in Chickpea Genotypes. Front. Plant Sci. 8:1375. P1 – 14. doi: 10.3389/fpls.2017.01375.

Pardales, J. J. R. and Kono, Y. (1990). Development of sorghum root system under increasing drought stress. Japan Journal of Crop Science 59:752_761 DOI 10.1626/jcs.59.752.

Parry, M. L., Rosenzweig, C., Iglesias, A., Livermore, M. and Fischer, G. (2004). Effects of climate change on global food production under SRES emissions and socio-economic scenarios. Global Environmental Change, 14, 53–67.

Passioura, J. B., Condon, A. G. and Richards, R. A. (1993). Water deficits, the development of leaf area and crop productivity. In: J. A. C. Smith and H. Griffith (Eds.), Water deficits plant responses from cell to community. Bioscience publishers Ltd., Oxford, UK, Pp 253-264.

Pastenes, C., Pimentel, P. and Lillo, J. (2005). Leaf movements and photoinhibition in relation to water stress in field-grown beans.

Patel, K. G., Thankappan, R., Mishra, G. P., Mandaliya, V. B., Kumar, A., Jentibhai, R. and Dobaria, J. R. (2017). Transgenic Peanut (*Arachis hypogaea* L.) Overexpressing *mtlD* Gene Showed Improved Photosynthetic, Physio-Biochemical, and Yield-Parameters under Soil-Moisture Deficit Stress in Lysimeter System. Front Plant Sci. 2017; Volume 8: doi: 10.3389/fpls.2017.01881.

Patil, A. and Lamnganbi, M. (2018). Impact of climate change on soil health A review International Journal of Chemical Studies 2018; 6(3): 2399-2404.

Pejić, B. Maksimović, L., Cimpeanu, S., Bucur, D., Milić, S.and Ćupina, B. (2011). Response of soybean to water stress at specific growth stages. Journal of Food, Agriculture & Environment Vol.9 (1): 280 – 284.

Peñuelas, J. and Filella, I. (1998). Visible and near-infrared reflectance techniques for diagnosing plant physiological status. *Trends in Plant Science* 3, 151–156.

Peoples, M. B., Hauggaard-Nielsen, H. and Jensen, E. S. (2009). The potential environmental benefits and risks derived from legumes in rotations. In: Emerich DW, Krishnan HB, editors. Nitrogen fixation in crop production. Madison: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America; 2009. p. 349–385.

Perignon, M., Vieux, F., Soler, L. G., Masset, G. and Darmon, N. (2017). Improving diet sustainability through evolution of food choices: review of epidemiological studies on the environmental impact of diets. Nutrition Reviews Vol. 75(1):2–17.

Petropoulos, S. A., Dimitra, Daferera, M. G. and Polissiou Passam, H. C. (2008). The effect of water deficit stress on the growth, yield and composition of essential oils of parsley. *J.Sci. Hort*. 115: 393–397.

Phillips, R. L. (2010). Mobilizing science to break yield barriers. Crop Sci. 50, S99–S108.

Pietragalla, J. and Pask, A. (2012). Stomatal conductance. In: Pask, A., Pietragalla, J., Mullan, D. and Reynolds, M. (Eds.) Physiological Breeding II: A Field Guide to Wheat Phenotyping. Mexico, D.F.: CIMMYT. p140.

Pingali, P. L. (2012). Green revolution: impacts, limits, and the path ahead. Proc. Natl. Acad. Sci. U.S.A. 109, 12302–12308.

Pinheiro, C., Chaves, M.M. and Ricardo, C. P. (2001). Alterations in carbon and nitrogen metabolism induced by water deficit in stem and leaves of Lupinus albus (L.). Journal of Experimental Botany 52, 1063–1070.

Pirnajmedin, F., Majidi, M. M. and Gheysari, M. (2015). Root and physiological characteristics associated with drought tolerance in Iranian tall fescue Euphytica. 202:141–155 DOI 10.1007/s10681-014-1239-5.

Polania, J., Rao, I. M., Cajiao, C., Grajales, M., Rivera, M., Velasquez, F. and Beebe, S. E. (2017). Shoot and root traits contribute to drought resistance in recombinant inbred lines of MD 23–24 9 SEA 5 of common bean. *Frontiers in Plant Science*, 8, 1–18. https://doi.org/10.3389/fpls.2017.00296.

Polania, J., Rao, I. M., Cajiao, C., Rivera, M., Raatz, B. and Beebe, S. (2016). Physiological traits associated with drought resistance in Andean and Mesoamerican genotypes of

common bean (Phaseolus vulgaris L.). Euphytica, 210, 17–29. https://doi.org/10.1007/s10681-016-1691- 5.

Praba, M. L., Cairns, J. E., Babu, R. C. and Lafitte, H. R. (2009). Identification of physiological traits underlying cultivar differences in drought tolerance in rice and wheat. J. Agron. Crop Sci. 195 30–46. 10.1111/j.1439-037X.2008.00341.x.

Prince, S. J., Mutava, R. N., Pegoraro, C., Oliveira, A. C. D. and Nguyen, H. T. (2013). Root characters. In *Genomics and Breeding for Climate Resilient Crops*; Kole, C. Ed.; Springer: Berlin, Germany, pp. 67–131.

Puangbut, D. Jogloy, S., Kesmala, T., Akkasaeng, C. and Patanothai, A. (2009). Variability in yield responses of peanut (Arachis hypogaea L.) genotypes under early season drought. Asian Journal of Plant Sciences 8(4); 254 – 264.

Purushothaman, R., Mainassara, Z. A., Nalini, M., Rajaram, P., Krishnamurthy, L. and Cholenahalli, L. G. (2013). Root anatomical traits and their possible contribution to drought tolerance in grain legumes. Plant Production Science 16, 1–8.

Qian, C., Yulong, Z., Zhanxiang, S., Jiaming, Z., Wei, B., Yue, Z., Yang, L., Liangshan, F., Chen, F., Zhe, Z., Ning, Y., Jochem, B. E. and Lizhen Z. (2017). Morphological plasticity of root growth under mild water stress increases water use efficiency without reducing yield in maize. Biogeosciences, 14, 3851–3858. https://doi.org/10.5194/bg-14-3851-2017.

Quan, S., Li, Y., Song, J., Zhang, T. and Wang, M. (2019) Adaptation to Climate Change and its Impacts on Wheat Yield: Perspective of Farmers in Henan of China. Sustainability, 11; 1-10. doi:10.3390/su11071928.

Raison, J. K. and Lyons, J. M. (1986). Chilling injury: a plea for uniform terminology. Plant Cell Environment. 9(9); 685 – 686.

Ramanjulu, S. and Bartels, D. (2002). Drought- and desiccation- induced modulation of gene expression in plants. Plant Cell and Environment, 25: 141–151.

Ramos, M. L. G., Parsns R., Sprent, J. I. and James, E. K. (2003). Effect of water stress on nitrogen fixation and nodule structure of common bean. *Pesquisa Agropecuiria Brasileira.* 38 (3):339-347.

Ranawake, A. L., Dahanayaka, N., Amarasingha, U. G. S., Rodrigo, W. D. R. J. and Rodrigo, U. T. D. (2011). Department of Agricultural Biology, Faculty of Agriculture, University of Ruhuna, Sri Lanka Effect of water stress on growth and yield of mung bean (*Vigna radiata* L.) Tropical Agricultural Research & Extension 14(4); p5.

Ranganayakulu, G. S., Sudhakar, C. and Reddy, P. S. (2015). Effect of water stress on proline metabolism and leaf relative Water content in two high yielding genotypes of groundnut (*Arachis hypogaea* L.) with contrasting drought tolerance Journal of experimental biology and agricultural sciences, 3: 97 – 103.

Rao, I. M. (2014). Advances in improving adaptation of common bean and Brachiaria forage grasses to abiotic stresses in the tropics. In: Pessarakli M (ed) Handbook of plant and crop physiology, 3rd edn. CRC Press, Taylor and Francis Group, Boca Raton, pp 847–889.

Rao, I. M., Miles, J. W., Beebe, S. E. and Horst, W. J. (2016). Root adaptations to soils with low fertility and aluminium toxicity. Ann Bot 118:593–605. doi:10.1093/aob/mcw073.

Ratnakumar, P. and Vadez, V. (2011). Groundnut (Arachis hypogaea L.) genotypes tolerant to intermittent drought maintain a high harvest index and have small leaf canopy under stress. Funct Plant Biol 38: 1016–1023.

Ray, D. K., Mueller, N.D., West, P. C., Jonathan A. and Foley, J. A. (2013). Yield Trends Are Insufficient to Double Global Crop Production by 2050**.** *PLoS ONE*, 8 (6): e66428 DOI: 10.1371/journal.pone.0066428.

Ray, J. D. and Sinclair, T. R. (1998). The effect of pot size on growth and transpiration of maize and soybean during water deficit stress. Journal of Experimental Botany 49(325): 1381-1386.

Reddy, A. R., Chaitanya, K. V. and Vivekanandan, M. (2004). Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. *J. Plant Physiol*. 161: 1189–1202.

Reddy, Y., Reddy, V. R. and Anbumozhi, V. (2003). "Physiological responses of groundnut (Arachis hypogaea L.) to drought stress and its amelioration: a critical review," Plant Growth Regulation, vol. 41, no. 1, pp. 75–88.

Rejeb, K. B., Abdelly, C. and Savouré, A. (2014). How reactive oxygen species and proline face stress together. Plant Physiology and Biochemistry 80; 278 – 284.

Reubens, B., Poesen, J., Danjon, F., Geudens, G. and Muys, B. (2007). The role of fine and coarse roots in shallow slope stability and soil erosion control with a focus on root system architecture: A review. *Trees*, *21*, 385–402.

Revoredo, C. L. and Fletcher, S. (2002). World Groundnut market: an overview of the past 30 years. Georgia Agricultural Experiment Stations, College of Agricultural and Environmental Sciences, the University of Georgia.

Richards, R. A., Condon, A. G. and Rebetzke, G. J. (2001). Traits to improve yield in dry environments. In Application of Physiology in Wheat Breeding; Reynolds, M.P., Ortiz-Monasterio, J. I., McNab, A., Eds.; CIMMYT: El Batan, Mexico; pp. 88–100.

Richardson, A. D., Duigan, S. P. and Berlyn, G. P. (2002). An evaluation of non-invasive methods to estimate foliar chlorophyll content. New Phytol. 153, 185–194.

Richardson, A.D., Duigan, S.P. and Berlyn, G.P. (2002). An evaluation of noninvasive methods to estimate foliar chlorophyll content. *New Phytologist* 153, 185–194.

Ringler, C., Zhu, T., Cai, E., Koo, J. and Wang, D. (2010). Climate Change Impacts on Food Security in Sub-Saharan Africa: Insights from Comprehensive Climate Change Scenarios. IFPRI Discussion Paper No. 1042. (Washington, DC: International Food Policy Research Institute, 2010).

Rodrigues, M. A. (2004). Establishment of continuous critical levels for indices of plant and preside dress soil nitrogen status in the potato crop. *Communications in Soil Science and Plant Analysis* 35: 2067–85.

Rosenzweig, C. and Iglesias, A. (eds.) (1993). Implications of Climate Change for International Agriculture: Crop Modeling Study. Washington, DC: US Environmental Protection Agency.

Rosenzweig, C. and Parry, M. L. (1994). Potential impact of climate change on world food supply. Nature 367:133–138.

Rowhani, P., Lobell, D. B., Linderman, M. and Ramankutty, N. (2011). Climate variability and crop production in Tanzania. *Agric. For. Meteorol.* 151, 449–460.

Rowland, D. L., Sorensen, R. B., Butts, C. L. and Faircloth, W. H. (2006). Determination of Maturity and Degree Day Indices and their Success in Predicting Peanut Maturity. Peanut Science 33:125-136. (62 -113 days)

Rucker, K. S., Kvien, C. K., Holbrook, C. C. and Hook, J. E. (1995). Identification of peanut genotypes with improved drought avoidance traits. Peanut Sci., 24: 14-18.

Sacks, M.M., Silk, W. K. and Burman, P. (1997). Effect of water stress on cortical cell division rates within the apical meristem of primary roots of maize. Plant Physiol., 114: 519–527.

Sade, N., Gebremedhin, A. and Moshelion, M. (2012). Risk-taking plants: anisohydric behavior as a stress-resistance trait. Plant Signal Behav 7(7): 767-770.

Sade, N., Vinocur, B. J., Diber, A., Shatil, A., Ronen, G., Nissan, H., Wallach, R., Karchi, H. and Moshelion, M. (2009). Improving plant stress tolerance and yield production: is the tonoplast aquaporin a key to isohydric to anisohydric conversion? New Phytol 181(3): 651-661.

Sadok, W. and Sinclair, T. R. (2011). Crops yield increase under water–limited conditions: review of recent physiological advances for soybean genetic improvement. Advances in Agronomy 113, 313–337.

Safarnejad, A. (2004). Characterization of soma clones of alfalfa (Medicago sativa L.) for drought tolerance. Journal of Agricultural Science and Technology, p121-127.

Saglam, A., Kadioglu, A., Demiralay, M. and TerzI, R. (2014). Leaf rolling reduces photosynthetic loss in maize under severe drought. Acta Bot. Croat. 73 (2), 315–332. DOI: 10.2478/botcro-2014-0012.

Sah, S. K., Reddy, K. R. and Li, J. (2016). Abscisic Acid and Abiotic StressTolerance in Crop Plants.Front. Plant Sci. 7:571.doi: 10.3389/fpls.2016.00571.

Sairam, R. K., Kumutha, D., Ezhilmathi, K., Deshmukh P.S., and Srivastava, G. C. (2008). Physiology and biochemistry of waterlogging tolerance in plants. Biologia Plantarum, 52(3): 401-412.

Sakakibara, H. (2006). Cytokinins: activity, biosynthesis, and translocation. Annu Rev Plant Biol.; 57:431-49.

Salunkhe, A. S., Poornima, R., Prince, K. S. J., Kanagaraj, P., Sheeba, J. A., Amudha, K., Suji, K.K., Senthil, A. and Babu, R.C. (2011). Fine mapping QTL for drought resistance traits in rice using bulk segregant analysis. *Mol. Biotechnol.*, *49*, 90–95.

Samarah, N. H., Alqudah, A. M., Amayreh, J. A. and Mcandrews, G. M. (2009). The effect of lateterminal drought stress on yield components of four barley cultivars. *J. Agron. Crop Sci.* 195: 427-441.

Sanders, T. H., Cole, R. J., Balnkenship, P. D. and Dorner, J. W. (1993). Aflatoxincontamination of peanuts from plants drought stressed in pod and root zones.Peanut Sci. 20, 5–8.

Sankar, B., Gopinathan, P., Karthishwaran, K. and Somasundaram, R. (2014).Variation in growth of peanut plants under drought stress condition and in combination with paclobutrazol and abscisic acid. Current Botany, 5: 14-21.

Sankar, B., Jaleel, C. A., Manivannan, P., Kishorekumar, A., Somasundaram, R. and Panneerselvam, R. (2007). Effect of paclobutrazol on water stress amelioration through antioxidants and free radical scavenging enzymes in *Arachis hypogaea* L. *J. Colloids Surf. B: Biointerfaces*. 60: 229–235.

Santoro, M. M., Liu, Y., Khan, S. M. A., Hou, L-X. and Bolen, D. W. (1992). Increased thermal stability of proteins in the presence of naturally occurring osmolytes. Biochemistry 31: 5278-5283.

Santos, R. C., Queiroz, C. M., Batista, V. G. L., Silva, C. R. C., Pinheiro, M. P. N., GalvãoFilho, A. L. A., Melo Filho, P. A. and Lima, L. M. (2013). Variabilidade de progênies F2 deamendoim geradas por meio de selec¸ ão de genitores ISSR-divergentes. RevistaCiência Agronômica 44, 578–586.

Saraswati, S. G. and Paliwal, K. (2011). Drought induced changes in growth, leaf gas exchange and biomass production in Albizia lebbeck and Cassia siamia seedlings. J. Environ. Biol. 32, 173- 178.

Savita, S. K., Kenchanagoudar, P. V. and Nadaf, H. L. (2014). Genetic variability for drought tolerance in advanced breeding lines of groundnut (*Arachis hypogaea* L.). Karnataka J. Agric. Sci., 27: 116-120.

Sayar, R., Khemira, H. and Kharrat, M. (2007). Inheritance of deeper root length and grain yield in half-diallel durum wheat (*Triticum durum*) crosses. Annalsof Applied Biology 151, 213–220.

Sazares, B. X., Ramirez- Ortega, F. A., Flores- Elenes, L. and Mendrano, R. R. (2011). Drought tolerance in crop plants. Am. J. Plant Physiol. 42, 173- 193.

Sazedur, R. and Ashfikur, R. (2019). "Impacts of Climate Change on Crop Production in Bangladesh: A Review," Journal of Agriculture and Crops, Academic Research Publishing Group, vol. 5(1), pages 6-14, 01-2019.

Schachtman, D. P. and Goodger, J. Q. *(*2008*). Chemical root to shoot signaling under drought.* Trends Plant Sci 13: 281–*287.*

Schachtman, D. P. and Shin R. (2007). Nutrient sensing and signaling: NPKS. Annu. Rev. Plant Biol., 58: 47-69.

Schneider, S. H. (1989). "The Changing Climate", *Scientific American* 261 (1989), p. 29.

Schonfeld, M. A., Johnson, R. C., Carver, B. F. and Mornhinweg, D. W. (1988). Water relations in winter wheat as drought resistance indicators. Crop Sci. 28: 526-531.

Schröder, W., Schmidt, G. and Schönrock, S. (2014). Modelling and mapping of plant phenological stages as bio-meteorological indicators for climate change. Environmental Sciences Europe, 26: (5); 1 – 13.

Sellin, A., (2001). Hydraulic and stomatal adjustment of Norway spruce trees to environmental stress. Tree Physiol. 21, 879–888.

Serraj, R. and Sinclair, T. R. (2002). Osmolyte accumulation: can it really help increase crop yield under drought condition: plant cell Environment. 25:333-341.

Shakeel, A. A., Xiao-yu, X., Long-chang, W., Muhammad, F. S., Chen, M. and Wang, L. (2011). Morphological, physiological and biochemical responses of plants to drought stress.

Shamsi, K. (2010). The effects of drought stress on yield, relative water content, proline, soluble carbohydrates and chlorophyll of bread wheat. Journal of Animal & Plant Sciences, cultivars Vol. 8, Issue 3: 1051- 1060.

Shamudzarira, Z. (1996). Water use and dry matter production in Sorghum and bambara groundnut. PhD thesis. University of Nottingham. UK. pp 190.

Sharada, P. and Naik, G. R. (2011). Physiological and biochemical responses of groundnut genotypes to drought stress. World J Sci Technol 1: 60-66.

Sharp, R. E., Poroyko, V., Hejlek, L. G., Spollen, W. G., Springer, G. K., Bohnert, H. J., Nguyen, H. T. (2004). Root growth maintenance during water deficits: physiology to functional genomics. J Exp Bot 55: 2343–2351.

Shashidhar, H.E., Henry, A. and Hardy, B. (Eds). (2012). Methodologies for root drought studies in rice. Los Baños (Philippines): International Rice Research Institute. 65 p.

Shavrukov, Y., Kurishbayev, A., Jatayev, S., Shvidchenko, V., Zotova, L., Koekemoer, F., de Groot, S., Soole, K. and Langridge, P. (2017). Early Flowering as a Drought Escape Mechanism in Plants: How Can It Aid Wheat Production? Frontiers in crop science doi: 10.3389/fpls.2017.01950.

Sheshshayee, M. S., Bindumadhava, H., Rachaputi, N. R., Prasad, T. G. M., Udayakumar, G. C. W. and Nigam, S. N. (2006). Leaf chlorophyll concentration relates to transpiration efficiency in peanut. Ann. Applied Biol., 148: 7-15.

Shiferaw, B., Tesfaye, K., Kassie, M., Prasanna, B. M. and Menkir, A. (2014). Managing vulnerability to drought and enhancing livelihood resilience in sub-Saharan Africa: Technological, institutional and policy options. Weather and Climate Extremes (3), 67 – 79.

Shrestha, R., Siddique, K. H. M., Turner, N. C., Turner, D. W. and Berger, J. (2005). Growth and seed yield of lentil (*Lens culinaris* Medikus) genotypes of West Asian and South Asian

origin and crossbreds between the two under rainfed conditions in Nepal. Australian Journal of Agricultural Research 56, 971–981.

Shumba-Mnyulwa, D. (2002). Promotion of bambara groundnut (*Vigna subterrannea*): Latest development of bambara groundnut research. Proceedings of the 2nd International Workshop of the International Bambara Groundnut Network, Sept. 23-25, International Plant Genetic Resources Institute, Nairobi, Kenya, pp: 17-19.

Sikuku, P. A., Netondo, G. W., Onyango, J. C. and Musyimi, D. M. (2010b). Chlorophyll fluorescence, protein and chlorophyll content of three NERICA rainfed rice varieties under varying irrigation regime. *Agricultural and Biological Science* 5(2): 19-25.

Sikuku, P. A., Netondo, G. W., Onyango, J. C. and Musyimi, D. M. (2010a). Effects of water deficit on physiology and Morphology of three varieties of nerica Rainfed rice (O*ryza sativa* L.) Journal of Agricultural and Biological Science, Vol. 5(1), 22 – 28. ISSN 1990-6145.

Sikuku, P. A., Onyango, J. C. and Netondo G. W. (2012). Physiological and biochemical responses of five nerica rice varieties (*Oryza sativa* L.) to water deficit at vegetative and reproductive stage. Agriculture and Biology Journal of North America Vol. 3(3): 93-104.

Sinclair, T. R, Tanner, C. B., Bennett, J. M. (1984). Water-use efficiency in crop production. Bio Science 34, 36–40.

Sinclair, T. R., Marrou, H., Soltani, A. and Valdez, V. (2014). Soybean production in Africa. *Glob. Food Biol.*, doi: 10.1016/j.fgs.20131.

Sinefu, F. (2011). Bambara groundnut response to controlled environment and planting date associated water stress. MSc Thesis. University of KwaZulu-Natal. p228.

Singh, A. L. (2003). Phenology of groundnut. Advances in Plant Physiology, Vol 6, Scientific Publishers (India), pp 295-382.

Singh, A. L. (2011). Physiological basis for realizing yield potentials in groundnut. In A. Hemantranjan (Ed.), Advances in plant physiology (Vol. 12, pp. 131–242). Jodhpur: Scientific Publishers (India).

Singh, V., van Oosterom, E. J., Jordan, D. R., Hunt, C. H. and Hammer, G. L. (2011). Genetic variability and control of nodal root angle in sorghum. Crop Science 51, 2011–2020.

Smirnoff, N. and Cumbes, Q. J. (1989). Hydroxyl radical scavenging activity of compatible solutes. Phytochemistry 28: 1057-1060.

Smith, M. R., Golden, C. D. and Myers, S. S. (2017). Potential rise in iron deficiency due to future anthropogenic carbon dioxide emissions. Geo Health; 1, 248–257.

Song, Y. H., Ito, S., and Imaizumi, T. (2013). Flowering time regulation: photoperiod- and temperature-sensing in leaves. Trends Plant Sci. 18, 575–583. doi: 10.1016/j.tplants.2013.05.003.

Songsri, P., Joglo, S., Vorasoot, N., Akkasaeng, C., Patanothai, A. and Holbrook, C. C. (2008). Root distribution of drought resistant peanut genotypes in response to drought. *Journal Agronomy & Crop Science* 194, 92–103. doi:10.1111/ j.1439-037X.2008.00296.x.

Songsri, P., Jogloy, S., Holbrook, C. C., Kesmala, T., Vorasoot, N., Akkasaeng, C. and Patanothai, A. (2009). Association of root, specific leaf area and SPAD chlorophyll meter reading

to water use efficiency of peanut under different available soil water. *Agricultural Water Management* 96 (5), 790–798.

Songsri, P., Jogloy, S., Junjittakarn, J., Kesmala, T., Vorasoot, N., Holbrook, C. C. and Patanothai, A. (2013). Association of stomatal conductance and root distribution with water use efficiency of peanut under different soil water regimes. Australian Journal of Crop Science 7, 948–955.

Soni, P. and Abdin, M. Z. (2017). Water deficit-induced oxidative stress affects artemisinin content and expression of proline metabolic genes in Artemisia annua L. FEBS Open Bio. 7(3): 367–381.

Sonneveld, B. G. J. S., Keyzer, M. A., Adegbola, P. and Pande, S. (2011). The Impact of Climate Change on Crop Production in West Africa: An Assessment for the Oueme River Basin in Benin. Water Resources Management. 26(2):553 - 579. https://doi.org/10.1007/s11269-011-9931-x.

Specht, J. E., Chase, K., Macrander, M., Graef, G. L., Chung, J., Markwell, J.P., Germann, M., Orf, H. H. and Lark, K. G. (2001). Soybean response to water: A QTL analysis of drought tolerance. Crop Sci. 41:493–509.

Sperry, J. S., Hacke, U. G., Oren, R. and Comstock, J. P. (2002). Water deficits and hydraulic limits to leaf water supply. Blackwell Science, Ltd Oxford, UK. Plant, Cell and Environment, 25, 251–263 10.1046/j.0016-8025.2001.00799.x.

Sponchiado, B. N., White, J. W., Castillo, J. A. and Jones, P. G. (1989). Root growth of four common bean cultivars in relation to drought tolerance in environments with contrasting soil types. Exp. Agr. 25: 249-257.

Sqiure, G. R., Connolly, H., Crawford, J., Collinson, S. T. and Sesay, A. (1996). Linking vegetative and reproductive trait variability in landraces of bambara groundnut. *In*: *Proceedings of the international bambara groundnut symposium*, University of Nottingham, UK, 201-213.

Srichaikul, B., Bunsang, R., Samappito, S., Butkhup S. and Bakker, G. (2011). Comparative study of chlorophyll content in leaves of Thai Morus alba Linn. Species. Plant Science Research, 3, 17-20.

Stagnari, F., Galieni, A., D'Egidio, S., Pagnani, G. and Pisante, M. (2017). Responses of radish to drought stress, Annals of Applied Biology. 172 (2); 170-186.

Stephens, J. M. (2012). *Bambara groundnut- (Voandzeia subterranea (L.) Thouars)*. Horticultural Sciences Department, Florida Cooperative Service, Institute of Food and Agricultural Sciences: University of Florida.

Stirling, C. M., Black, C. R. and Ong, C. K. (1989). The Response of Groundnut (Arachis hypogaea L.) to Timing of Irrigation: II. ^{14} C-Partitioning and Plant Water Status. Journal of Experimental Botany, 40 (221): 1363-1373.

Stucky, B. J., Guralnick, R., Deck, J., Denny, E. G., Bolmgren, K. and Walls, R. (2018). The Plant Phenology Ontology: A New Informatics Resource for Large-Scale Integration of Plant Phenology Data. Front. Plant Sci. 9:517. doi: 10.3389/fpls.2018.00517.

Subbarao, G., Johansen, C., Slinkard, A. E., Nageswara Rao, R. C., Saxena, N. P., Chauhan, Y. S. and Lawn, R. J. (1995). Strategies for improving drought resistance in grain legumes. *Crit. Rev. Plant Sci. 14*, 469–523.

Sukanya, M. and Mahendran, S. (2018). Impact of moisture stress at flowering stage on the growth and yield of selected groundnut (Arachis hypogaea L.) cultivars. International Journal of Research Publications. Volume-4, Issue-1, p1-10. DOI: 1004152018121.

Sumner, G. N. (1983). The use of correlation linkages in the assessment of daily rainfall patterns. J. Hydrol. 66; 169–181.

Suneet, K. G. (2016). Comparison of the leaf parameters and transpiration rate in commonly grown exotic and indigenous tress species in India during the active transpiration period. Int. J. Bot. Res. 4, 13-16.

Suwanprasert, J., Toojinda, T., Srinives, P. and Chanprame, S. (2006). Hybridization Technique for Bambara Groundnut. Breeding Science 56: 125–129.

Swanevelder, C. (1998). *Bambara–food for Africa*; National Department of Agriculture, Government Printer: Pretoria, Republic of South Africa. p16.

Taiz, L. and Zeiger, E. (2006). Stress physiology In: Plant Physiology, 4th edition, Edited by Sinauer Associates, Inc., Sunde MA. p671–681.

Taiz, L. and Zieger, E. (1998). Stress Physiology. In: Plant Physiology, 2nd edn. Sinauer Associates, Inc., Sunderland, M.A. pp. 725-757.

Talebi, R. (2011). Evaluation of chlorophyll content and canopy temperature as indicators for drought tolerance in durum wheat. *Aust. J. of Basic and App. Sci*. 5(11), 1457-1462.

Tambussi, E. A., Bort, J. and Araus, J. L. (2007). "Water use efficiency in C3 cereals under Mediterranean conditions: a review of physiological aspects". Annals of Applied Biology. 150 (3): 307–321. doi:10.1111/j.1744-7348.2007.00143.x.

Taru, V. B., Kyagya, I. Z. and Mshelia, S. I. (2010). Profitability of groundnut production in Michika Local Government Area of Adamawa State, Nigeria. *Journal of Agricultural Science* 1(1): 25 – 29.

Tátrai, Z. A., Sanoubar, R., Pluhár, Z., Mancarella, S., Orsini, F. and Gianquinto, G. (2016) Morphological and Physiological Plant Responses to Drought Stress in Thymus citriodorus. International Journal of Agronomy, pp 1-8.

Tekle, A. T. and Alemu, M. A. (2016). Drought Tolerance Mechanisms in Field Crops. World Journal of Biology and Medical Sciences, Volume 3, Issue- 2, 15-39.

Thangthong, N., Jogloy, S., Jongrungklang, N., Kvien, C. K., Pensuk, V. Kesmala, T. and Vorasoot, N. (2017). Root distribution patterns of peanut genotypes with different drought resistance levels under early-season drought stress. Journal of Agronomy andCrop Science DOI: 10.1111/jac.12249).

Thompson, D. W. J., Barnes, E. A., Deser, C., Foust, W. E. and Phillips, A. S. (2015). Quantifying the role of internal climate variability in future climate trends. *J. Clim.* 28, 6443–6456.

Thottappilly, G. and Rossel, H. (1997). Identification and characterization of viruses infecting Bambara groundnut (Vigna subterranea) in Nigeria. International Journal of Pest Management, 43: 177-185.

Tindall, H. D. (1997). Vegetables in the Tropics, Macmillan Education Ltd.

Tombesi, S., Nardini, A., Frioni, T., Soccolini, M., Zadra, C., Farinelli, D., Poni, S. and Palliotti, A. (2015). Stomatal closure is induced by hydraulic signals and maintained by ABA in drought-stressed grapevine.*Scientific Reports*, 5, 12449.

Trachsel, S., Kaeppler, S. M., Brown, K. M. and Lynch, J. P. (2011). Shovelomics: High throughput phenotyping of maize root architecture in the field. *Plant Soil*, *341*, 75–87.

Tsoata, E., Njock, S. R., Youmbi, E. and Nwaga, D. (2015). Early effects of water stress on some biochemical and mineral parameters of mycorrhizal Vigna subterranea (L.) Verdc (Fabaceae) cultivated in Cameroon. International Journal of Agronomy and Agricultural Research, Vol. 7, No. 2, p. 21-35.

Tuberosa, R. (2012) Phenotyping for drought tolerance of crops in the genomics era. Front. Physiol. 3, 347.

Turner, N. C. (1986). Crop water deficits: a decade of progress. Advances in Agronomy 39, 1-51.

Turner, N. C., Wright, G. C. and Siddique, K. H. M. (2001). Adaptation of grain legumes pulses to water-limited environments, *Adv. Agron.,* 71: 123–231.

Turner, N.C. and Jones, M.M. (1980). Turgor maintenance by osmotic adjustment: A review and evaluation. In: *Adaptation of Plants to Water and High Temperature Stress*, Turner, N.C. and Kramer, P. J. eds. New York, J. Wiley & Sons, pp. 87–103.

Tweneboah, C. K. (2000). Modern agriculture in the tropics, Food crops. Co-wood Publishers. pp. 189-190.

Uga, Y., Kitomi, Y., Ishikawa, S. and Yano, M. (2015). Genetic improvement for root growth angle to enhance crop production. Breeding Science 65: 111–119.

Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Hara, N., Kitomi, Y., Inukai, Y., Ono, K., Kanno, N., Inoue, H., Takehisa, H., Motoyama, R., Nagamura, Y., Wu, J., Matsumoto, T., Takai, T., Okuno, K. and Yano, M. (2013). Control of root system architecture by

DEEPER ROOTING 1 increases rice yield under drought conditions. Nat. Genet. 45: 1097–1102.

UN (United Nations). (2017). World population prospects. https://www.un.org/development/desa/en/news/population/world-population-prospects (Site visited on 06 February 2019).

UNFCCC (United Nations Framework Convention on Climate Change). (2006). Handbook. United Nations Framework Convention on Climate Change. Bonn, Germany: Climate Change Secretariat, Produced by Intergovernmental and Legal Affairs, Climate Change Secretariat. pp216.

USCB (United States Census Bureau). (2014). International database, June 2011 update. http://www.census.gov/population/international/data/idb/worldpoptotal.,php (accessed 8 April 2016).

USDA (United States Department of Agriculture). (2009). Access to Affordable and Nutritious Food: Measuring and Understanding Food Deserts and Their Consequences, U.S. Department of Agriculture, Economic Research Service. Report to Congress, http://www.ers.usda.gov/Publications/AP/AP036/.

USDA (United States Department of Agriculture). (2011). Foreign Agricultural service. Circular Series WAP 1111," http://www.fas.usda.gov/psdonline/circulars/production.pdf.

US-EPA (United States Environmental Protection Agency). (2017). Climate Change Impacts. www.epa.gov (Site visited on 26 January 2019).

USGCRP (United States Global Change Research Program). (2014). Climate Change Impacts in the United States: The Third National Climate Assessment. [Melillo, Jerry M., Terese

(T. C.) Richmond, and Gary W. Yohe, (Eds.)], U.S. Global Change Research Program, 841 pp. doi: 10.7930/J0Z31WJ2.

Vadez, V., Rao, J. S., Bhatnagar-Mathur, P. and Sharma, K. K. (2013). DREB1A promotes root development in deep soil layers and increases water extraction under water stress in groundnut. Plant Biol.; 15, 45–52.

Vaidya, S., Vanaja, M., Lakshmi, N.J., Sowmya, P., Anitha, Y. and Sathish, P. (2015). Variability in Drought Stress Induced Responses of Groundnut (*Arachis hypogaea* L.) Genotypes. Biochemistry and Physiology. 4(1) DOI: 10.4172/2168-9652.1000149.

Van der Mescht, A., De Ronde, J. A. and Rossouw, F. T. (1999). Chlorophyll fluorescence and chlorophyll content as a measure of drought tolerance in potato. *South African Journal of Science* 95 (9), 407–412.

Varshney, R. K., Mahendar, T., Aruna, R., Nigam, S. N., Neelima, K., Vadez, V. and Hoisington, D. A. (2009). High level of natural variation in a groundnut (Arachis hypogaea L.) germplasm collection assayed by selected informative SSR markers. *Plant Breeding*, *128*, 486–494.

Varshney, R. K., Pazhamala, L., Kashiwagi, J., Gaur, P.M., Krishnamurthy, L. and Hoisington, D. (2011). Genomics and physiological approaches for root trait breeding to improve drought tolerance in chickpea (Cicer arietinum L.). In: Costa de Oliveira A, Varshney RK, eds. Root genomics. Dordrecht, The Netherlands: Springer, 233–250.

Vendruscolo, A. C. G., Schuster, I., Pileggi, M., Scapim, C. A., Molinari, H. B. C., Marur, C. J. and Vieira, L. G. C. (2007). Stress-induced synthesis of proline confers tolerance to water deficit in transgenic wheat. J. Plant Physiol., 164(10): 1367-1376.

Vernieri, P., Pardossi, A. and Tognoni, F. (1991). Influence of chilling and drought on water relations and abscisic acid accumulation in bean. Australian Journal of Plant Physiology. vol. 18, No. 1, p. 25–35.

Viehweger, K. (2013). How plants cope with heavy metals. - Bot. Studies 55: 1-12, 2014.

Voisin, A. S., Guéguen, J., Huyghe, C., Jeuffroy, M. H., Magrini, M. B., Meynard, J. M., et al. (2014). Legumes for feed, food, biomaterials and bioenergy in Europe: a review. Agron Sustain Dev. 34:361–80.

Vorasoot, N., Songsri, P., Akkasaeng, C., Jogloy, S. and Patanothai, A. (2003). Effect of water stress on yield and agronomic characters of peanut (Arachis hypogaea L.). Songklanakarin J. Sci. Technol. 25, 283–288.

Vurayai, R., Emongor, V. and Moseki, B. (2011a). Physiological responses of bambara groundnut (Vigna subterranea (L.) Verdc) to short periods of water stress during different development stages. Asian J Agric Sci 3:37–43.

Vurayai, R., Emongor, V. and Moseki, B. (2011b). Effect of Water Stress Imposed at Different Growth and Development Stages on Morphological Traits and Yield of Bambara Groundnut (Vigna subterranea L. Verdc). American Journal of Plant Physiology, 6(1): 17 – 27.

Vyas, S. S., Bhattacharya, B. K., Nigam, R., Guhathakurta, P., Ghosh, K., Chattopadhyay, N. and Gairola, R. (2015). A combined deficit index for regional agricultural droughtassessment over semi-arid tract of India using geostationary meteorologicalsatellite data. Int. J. Geogr. Inf. Sci. 39, 28–39.

Waele, D. and Swanevelder, C. J. (2001). Crop production in tropical Africa. Goikink Graphic nv. Belgium. pp747-753.

Walter, A., Studer, B. and Kölliker, R. (2012). Advanced phenotyping offers opportunities for improved breeding of forage and turf species Annals of Botany 110: 1271–1279.

Wassermann, V. D., Kruger, A. J. and Heyns, G. (1984). The response of Bambara groundnut (*Voandzeia subterranea* L. Verdc) and pigeon pea (*Cajanus cajan*) to applications of lime, P and K, South African Journal of Plant and Soil, 1:1, 4-8, DOI:10.1080/02571862.1984.10634100.

Wasson, A. P., Richards, R. A., Chatrath, R., Misra, S. C., Prasad, S. V., Rebetzke, G. J., Kirkegaard, J. A., Christopher, J. and Watt, M. (2012). Traits and selection strategies to improve root systems and water uptake in water limited wheat crops. Journal of Experimental Botany 63, 3485–3498.

Weiss, A., Van Crowder, L. and Bernardi, M. (2000). Communicating agrometeorological information to farming communities. *Agricultural Forest Meteorology* 103: 185–196.

Werner, D. and Newton, W. E. (2005). Nitrogen fixation in agriculture, forestry, ecology, and the environment. Volume 4 of Nitrogen Fixation: Origins, Applications and Research Progress. Springer, Dordrecht. 347 p.

Wheeler, T. and von Braun, J. (2013). Climate change impacts on food security. Science 341, 508–513.

Wilhite, D. A. and Glantz, M. H. (1985). Understanding the Drought Phenomenon: The Role of Definitions. *Water International* 10(3):111–120.

Williams, J. H., Hilderband, G. L. and Tattersfield, J. R. (1978). The effect of weather and genotype X environment interaction on the yields of groundnut (Arachis hypogaea. L.). Rhod. J. Agri. Res. 16: 193-204.

Wilson, J. B. (1988). A review of evidence on the control of shoot: root ratio, in relation to models. Ann Bot 61:433–449.

Wind, J., Smeekens, S. and Hanson, J. (2010). Sucrose: metabolite and signaling molecule. Phytochemistry 71:1610–1614.

WMO (World Meteorological Organization). (2006). Drought monitoring and early warning: concepts, progress and future challenges. World Meteorological Organization. No.1006, pp 26.

Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., et al. (2012). Warming experiments underpredict plant phenological responses to climate change. Nature 485, 494–497. doi: 10.1038/nature11014.

Wopereis, M. C. S., Kropff, M. J., Maligaya, A. R. and Tuong, T. P. (1996). Drought-stress responses of two lowland rice cultivars to soil water status. Field Crops Research 46, 21-39.

WRI (World Resources Institute). (1996). World Resources: A Guide to Global Environment, 1996-1997. World Resources Institute, United Nations Environment Program, World Bank, Oxford University Press.

WRI (World Resources Institute). (1998). World Resources: A guide to the global environment 1998-199. World Resources Institute, environmental change and human health (English). Washington, D.C., The World Bank.

http://documents.worldbank.org/curated/en/545461468744003084/World (visited on November 2018).

Wright, G. C. and Nageswara Rao, R. C. (1994). Groundnut water relations. In: The *Groundnut Crops Smartt J* (Ed). Chapman and Hall, London, pp: 281-235.

Wu, Y. and Cosgrove, D. J. (2000). Adaptation of roots to low water potentials by changes in cell wall extensibility and cell wall proteins. J. Exp. Bot., 51: 1543-1553.

Wyn Jones, R. G., Storey, R., Leigh, R. A., Ahmad, N. and Pollard, A. (1977). A hypothesis on cytoplasmic osmoregulation. In "Regulation of Cell Membrane Activities in Plants" (E. Marre, O. Cifferi eds), Elsevier, Amsterdam, pp. 121-136.

Wyn Jones, R.G. and Gorham, J. (1983). Osmoregulation. In Encyclope-dia of Plant Physiology, Vol. 12C. Responses to the Chemical andBiological Environment. Springer-Verlag, Heidelberg, pp35--58.

Xiong, L., Wang, R. G., Mao, G. and Koczan, J. M. (2006). Identification of drought tolerance determinants by genetic analysis of root responses to drought stress and abscisic acid. Plant Physiology. 142: 1065-1074.

Yadav, R. S., Hash, C. T., Bidinger, F. R., Devos, K. M. and Howarth, C. J. (2004). Genomic regions associated with grain yield and aspects of post flowering drought tolerance in pearl millet across environments and tester background. Euphytica, 136: 265-277.

Yaish, M. W. (2015). Proline accumulation is a general response to abiotic stress in the date palm tree (*Phoenix dactylifera* L.). Genetics and Molecular Research 14 (3): 9943-9950.

Yamada, M., Morishita, H., Urano, K., Shiozaki, N., Yamaguchi-Shinozaki, K., Shinozaki, K. and Yoshiba, Y. (2005). Effects of free proline accumulation in petunias under drought stress. J Exp Bot 56, 1975–1981.

Yamaguchi, M. and Sharp, R .E. (2010). Complexity and coordination of root growth at low water potentials: recent advances from transcriptomic and proteomic analyses. Plant Cell Environ 33: 590–603.

Yancey, P. H. (1994). Compatible and counteracting solutes. In "Cellular and Molecular Physiology of Cell Volume Regulation" (K Strange ed), CRC Press, Boca Raton, pp. 81-109.

Yang, Z., Hai, B., Qin, L., Ti, X., Shangguan, L., Zhao, Y., Wiggins, L., Liu, Y., Feng, J. Q., Chang, J. Y., Wang, F. and Liu, F. (2013). Cessation of epithelial bmp signaling switches the differentiation of crown epithelia to the root lineage in a β-catenin-dependent manner. *Mol. Cell. Biol.* 33, 4732-4744. 10.1128/MCB.00456-13.

Yao, D. N., Kouassi, K. N, Erba, D., Scazzina, F., Pellegrini, N., et al. (2015). Nutritive evaluation of the bambara groundnut Ci12 landrace [Vigna subterranea (L.) Verdc (Fabaceae)] produced in Côte d'Ivoire. Int J Mol Sci 16(9): 21428-21441.

Yasmin, S. and Nehvi, F. A. (2018). Phenological Growth Stages of Saffron (*Crocus sativus* L.) under Temperate Conditions of Jammu & Kashmir-India *Int.J.Curr.Microbiol.App.Sci* *7*(4): 3797-3814.

Ye, H. Roorkiwal, M., Valliyodan, B., Zhou, L., Chen, P., Varshney, R. K. and Nguyen, H. T. (2018). Genetic diversity of root system architecture in response to drought stress in grain legumes. Journal of Experimental Botany doi:10.1093/jxb/ery082.

Yordanov, I., Velikova, V. and Tsonev, T. (2003). Plant responses to drought and stress tolerance. Bulg. J. Plant Physiol. Special Issue 2003, 187–206.

Yu, L. X., Ray, J. D., O'Toole, J. C. and Nguyen, H. T. (1995). Use of wax–petrolatum layers for screening rice root penetration. Crop Science 35, 684–687.

Zaman-Allah, M., Jenkinson, D. M. and Vadez, V. (2011). Chickpea genotypes contrasting for seed yield under terminal drought stress in the field differ for traits related to the control of water use. Functional Plant Biology 38, 270–281. doi:10.1071/FP10244.

Zenis, A., Kantartzi, S., Meksem, K. and Kassem, My-A. (2016). Influence of Drought Stress on Several Root Traits and their Correlation with Seed Protein and Oil Contents in Soybean. Atlas Journal of Biology. pp. 267–273. doi: 10.5147/ajb.2016.0140.

Zhang, M., Duan, L., Zhai, Z., Li, J., Tian, X., Wang, B., He, Z. and Li, Z. (2004). Effects of plant growth regulators on water deficit-induced yield loss in soybean. *Proceedings of the 4th International Crop Science Congress,* Brisbane, Australia.

Zhang, X., Ervin, E. H., Evanylo, G. K. and Haering, K. C. (2009). Impact of biosolids on hormone metabolism in drought-stressed tall fescue. Crop Sci. 49:1893–1901.

Zhao, C., Liu, B., Piao, S., Wang, X., Lobell, D. B., Huangj, Y., Huang, M., Yao, Y., Bassu, S., Ciais, P., Jean-Louis, D., Elliott, J., Ewert, F., Janssens, I. A., Li, T., Lin, E., Liu, Q., Martre, P., Müller, C., Peng, S., Peñuelas, J., Ruane, A. C., Wallach, D., Wang, T., Wu, D., Liu, Z., Zhu, Y., Zhu, Z. and Asseng, S. (2017). Temperature increase reduces global yields of major crops in four independent estimates. PNAS; vol. 114; no. 35, 9326–9331.

Zhao, J., Fu, J., Liao, H., He, Y., Nian, H., Hu, Y., Qiu, L., Dong, Y. and Yan, X. (2004). Characterization of root architecture in an applied core collection for phosphorus efficiency of soybean germplasm. *Chin. Sci. Bull.*, *49*, 1611–1620.

Zhao, T. J., Sun, S., Liu, Y., Liu, J. M., Liu, Q., Yan, Y. B. and Zhou, H.M. (2006). Regulating the drought-responsive element (DRE)-mediated signaling pathway by synergic functions of trans-active and transinactive DRE binding factors in *Brassica napus*. J. Biol. Chem., 281: 10752-10759.

Zhao, W., Sun, Y., Kjelgren, R. and Liu, X. (2015). Response of stomatal density and bound gas exchange in leaves of maize to soil water deficit. Acta Physiol Plant. (37): 1-9. DOI 10.1007/s11738-014-1704-8.

Zheng, H. G., Babu, R. C., Pathan, M. S., Ali, L., Huang, N., Courtois, B. and Nguyen, T. (2000). Quantitative trait loci for root-penetration ability and root thickness in rice: comparison of genetic backgrounds. Genome 43, 53–61.

Zhou, Y., Lambrides, C. J. and Shu, F. (2014). Drought resistance and soil water extraction of a perennial C4 grass: contributions of root and rhizome traits. Funct. Plant Biol 41, 505–519.

Zhu, C., Kobayashi, K., Loladze, I., Zhu, J., Jiang, Q., Xu, X., Liu, G., Seneweera, S., Ebi, K. L., Drewnowski, A., Fukagawa, N. K. and Ziska, L. H. (2018). Carbon dioxide (CO_2) levels this century will alter the protein, micronutrients, and vitamin content of rice grains with potential health consequences for the poorest rice-dependent countries. Sci. Adv. (4): eaaq1012.

Zhu, J., Ingram, P. A., Benfey, P. N. and Elich, T. (2011). From lab to field, new approaches to phenotyping root system architecture. Curr. Opin. Plant Biol., 14, 310–317.

Zondi, L. Z. (2012). Responses of bambara groundnut (*vigna subterannea* [L.] Verdc) landraces to field and controlled Environment conditions of water stress. MSc Thesis. University of KwaZulu-Natal Pietermaritzburg South Africa. p189.

Zougmoré, R., Mando, A. and Stroosnijder, L. (2004). Effect of Soil and Water Conservation and Nutrient Management on the Soil-plant Water Balance in Semi-arid Burkina Faso. Agr. Water Manage, 65 (2):103-120.

Appendices

Appendix 1: Sum of squares from the combined ANOVA for leaf proline content, relative leaf water content and chlorophyll content index during flowering and pod development water deficit stress in 2017 and 2018 cropping seasons.

			Proline				Relative water content				Chlorophyll content index			
			S1		S2		S1		S2		S1		S2	
	SOV	D.F.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.
Bambara	Year (Y)	1	0.44932	0.026	0.19135	0.116	2.1947	0.097	0.172	0.785	0.1768	0.356	0.0234	0.803
groundnut	Replication	2	0.32291		0.01186		2.0999		2.371		1.4964		0.0725	
landraces	Water regime (WR)	2	253.35351	<.001	216.52585	<.001	7380.9205	<.001	6141.568	<.001	74.7936	0.002	78.6452	<.001
	Landrace (L)	2	15.90017	<.001	35.06486	<.001	532.7802	<.001	326.942	<.001	492.7334	<.001	393.484	<.001
	WR x L	4	20.38004	<.001	26.13972	<.001	336.9364	<.001	249.417	<.001	3.6837	0.033	13.5716	0.008
	WR x Y	2	1.25707	0.003	0.01989	0.869	4.5449	0.066	5.979	0.287	0.0527	0.876	1.004	0.28
	L x Y	2	0.02289	0.861	0.03541	0.78	2.3038	0.228	1.045	0.794	1.1132	0.086	0.6418	0.435
	WR x L x Y	4	0.09944	0.856	0.28814	0.421	13.1433	0.01	8.521	0.456	0.8985	0.37	5.8145	0.018
	Pooled error	53	293.82658		280.17074		8322.2257		6811.878		584.4752		507.9676	
MNANJE	Year (Y)	1	5.7576	<.001	0.15806	0.132	8.216	0.103	4.686	0.196	1.2904	0.271	7.6296	<.001
(Groundnut)	Replication	2	0.4899		0.21365		4.558		3.293		0.7208		3.0111	
	Water regime (WR)	2	262.8715	<.001	35.61232	<.001	1379.84	<.001	1876.284	<.001	27.2971	0.013	34.8799	<.001
	WR x Y	2	0.8783	0.091	1.98602	0.002	45.464	0.012	12.89	0.131	3.2345	0.238	1.3333	0.037
	Pooled error	17	271.0491		38.53605		1453.449		1912.517		41.277		48.6369	

SOV = Source of variation, D.F = Degrees of freedom, F pr. = Probability, S.S = Sum of squares, S1 = Stress during flowering, S2 = Stress during pod development

Appendix 2: Sum of squares from the combined ANOVA for photosynthesis rate, stomatal conductance and transpiration rate during flowering and pod development water deficit stress and water use efficiency (WUE) at harvest in 2017 and 2018 cropping seasons.

			Photosynthesis rate				Stomatal conductance				Transpiration rate				WUE		Grain yield (t ha-1)	
			S1		S2		S1		S2		S1		S2		At harvest			
	SOV	D.F.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr	S.S.	F pr
Bambara groundnut landraces	Year (Y)	1	10.16	0.137	2.46	0.061	0.00019	0.817	0.004601	0.013	2.88	0.22	0.10254	0.249	0.00032	0.596	0.001552	0.632
	Replication	2	4.85		0.91		0.0204		0.000682		3.7		0.43269		0.19531		0.016025	
	Water regime (WR)	2	38985.35	<.001	10801.76	<.001	36.56537	<.001	0.573558	<.001	3202.15	<.001	77.67934	<.001	3.05943	<.001	14.231746	<.001
	Landrace (L)	2	4193.34	<.001	6769.23	<.001	16.64476	<.001	0.349248	<.001	186.26	<.001	48.37738	<.001	0.07069	<.001	5.247252	<.001
	WR x L	4	842.35	<.001	3645.15	<.001	7.92622	<.001	0.109697	<.001	112.02	<.001	2.79888	<.001	0.00009	<.001	0.573331	<.001
	WR x Y	2	41.02	0.02	7.58	0.009	0.02748	0.036	0.004235	0.051	1.94	0.589	0.19606	0.283	0.00168	0.092	0.003856	0.748
	L x Y	2	24.2	0.081	9.26	0.004	0.04723	0.006	0.000314	0.774	0.53	0.863	0.01628	0.894	0.00038	0.555	0.015566	0.327
	WR x L x Y	4	38.51	0.098	13.16	0.005	0.08037	0.003	0.000649	0.894	0.79	0.977	0.03945	0.967	0.0012	0.449	0.033327	0.317
	Pooled error	53	44340.86		21286.54		61.51605		1.0582		3553.66		132.33831		3.34184		20.319897	
MNANJE (Groundnut)	Year (Y)	1	99.98	<.001	0.57	0.588	0.00004	0.959	0.001037	0.352	0.21	0.625	0.1259	0.375	0.00269	0.806	0.000381	0.803
	Replication	2	4.54		3.25		0.0102		0.000026		0.01		0.0766		0.51825		0.011084	
	Water regime (WR)	2	47963.81	<.001	3888.47	<.001	59.17861	<.001	0.205105	<.001	1836.46	<.001	22.8552	<.001	0.00025	<.001	13.244015	<.001
	WR x Y	2	86.61	0.002	2.77	0.497	0.04697	0.291	0.000791	0.694	0.68	0.672	0.0055	0.98	0.00073	0.712	0.002835	0.784
	Pooled error	17	48197.98		3908.42		59.36584		0.21436		1845.79		24.1012		0.53556		13.306443	

SOV = Source of variation, D.F = Degrees of freedom, F pr. = Probability, S.S = Sum of squares, S1 = Stress during flowering, S2 = Stress during pod development

Appendix 3: Sum of squares from the combined ANOVA for plant height, canopy spread and root: shoot ratio during flowering and pod development water deficit stress in 2017 and 2018 cropping seasons.

			Plant height				Canopy spread				Root: Shoot ratio			
			S1		S2		S1		S2		S1		S2	
	SOV	D.F.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.
Bambara	Year (Y)	1	23.08	<.001	4.74	0.032	0	0.978	0.03	0.879	0	0.97	0.00002	0.477
groundnut	Replication	2	2.06		3.54		1.67		0.24		0		0.00004	
landraces	Water regime (WR)	2	18.57	0.036	32.35	0.024	915.89	<.001	1914.29	<.001	0.00242	<.001	0.00113	0.04
	Landrace (L)	2	234.45	<.001	99.97	<.001	93.23	<.001	61.91	0.004	0.00346	<.001	0.00549	<.001
	WR x L	4	7.31	0.03	16.67	0.083	41.1	<.001	623.77	<.001	0.0003	0.003	0.00271	<.001
	WR x Y	2	0.16	0.891	1.26	0.503	1.38	0.486	6.08	0.14	0.00001	0.677	0.00012	0.163
	L x Y	2	4.41	0.063	3.96	0.135	3.68	0.164	0.39	0.868	0.00001	0.801	0.0001	0.2
	WR x L x Y	4	0.68	0.906	0.89	0.904	2.05	0.697	18.54	0.032	0.00004	0.575	0.00043	0.023
	Pooled error	53	312.98		203.86		1102.16		2694.14		0.00658		0.01162	
MNANJE	Year (Y)	1	7.373	0.101	0.056	0.816	0.109	0.754	1.445	0.592	0.0003	0.976	0	0.892
(Groundnut)	Replication	2	2.183		0.068		2.534		1.188		1.1283		0.00006	
	Water regime (WR)	2	206.3	0.001	174.8	<.001	749.91	<.001	381.65	<.001	26.95	0.001	0.00138	0.002
	WR x Y	2	3.188	0.488	0.431	0.802	1.834	0.453	1.863	0.819	0.1144	0.854	0.00001	0.858
	Pooled error	17	238		185.6		763.82		416.03		31.326		0.00161	

SOV = Source of variation, D.F. = Degrees of freedom, F pr. = Probability, S.S. = Sum of squares, S1 = Stress during flowering, S2 = Stress during pod development.

Appendix 4: Sum of squares from the combined ANOVA rooting depth, root surface area, average root diameter during flowering and pod development water deficit stress in 2017 and 2018 cropping seasons.

			Rooting depth				Root surface area				Average root diameter			
			S1		S2		S1		S2		S1		S2	
	SOV	D.F.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.
Bambara	Year (Y)	1	2.95	0.374	20.51	0.029	52.73	0.117	662.80	0.069	0.00019	0.421	0.03756	0.055
	Replication	2	0.80		5.62		62.59		213.60		0.00009		0.00455	
	Water regime (WR)	2	3059.99	<.001	1042.48	<.001	70448.15	<.001	381652.50	<.001	0.21749	<.001	0.37994	0.006
	Landrace (L)	2	6849.21	<.001	6409.61	<.001	628757.35	<.001	992617.10	<.001	0.04579	<.001	1.43300	<.001
	WR x L	4	239.97	<.001	142.76	<.001	17708.97	<.001	21635.80	<.001	0.02250	<.001	0.08498	0.018
	WR x Y	2	11.93	0.213	22.44	0.072	18.88	0.624	36.90	0.902	0.00217	0.041	0.02640	0.211
	L x Y	2	13.20	0.183	17.30	0.123	80.59	0.155	145.20	0.671	0.00396	0.006	0.01607	0.376
	WR x L x Y	4	44.42	0.04	24.43	0.201	88.82	0.369	1790.50	0.077	0.00124	0.388	0.02955	0.458
	Pooled error	53	10347.77		7789.43		718004.31		1408329.50		0.30170		2.24101	
MNANJE	Year (Y)	1	319.20	<.001	408.03	<.001	98.36	0.13	49.00	0.34	0.00543	<.001	0.013246	0.049
(Groundnut)	Replication	2	8.03		0.40		135.10		1237.29		0.00021		0.007891	
	Water regime (WR)	2	827.95	<.001	173.02	<.001	87622.82	<.001	301383.88	<.001	0.05506	<.001	0.362103	0.002
	WR x Y	2	1.92	0.683	11.15	0.098	24.85	0.694	193.70	0.201	0.00067	0.184	0.008632	0.22
	Pooled error	17	1191.10		603.05		88150.73		305959.72		0.06302		0.420088	

SOV = Source of variation, D.F. = Degrees of freedom, F pr. = Probability, S.S. = Sum of squares, S1 = Stress during flowering, S2 = Stress during pod development.

Appendix 5: Sum of squares from the combined ANOVA for total root length, root volume and root length density during flowering and pod development water deficit stress in 2017 and 2018 cropping seasons.

			Total root length				Root volume				Root length density			
			S1		S2		S1		S2		S1		S2	
	SOV	D.F.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.	S.S.	F pr.
Bambara	Year (Y)	1	488.7	0.456	42579	0.002	0.37682	0.013	0.0276	0.852	110	0.514	38.64	0.358
groundnut	Replication	2	1965.5		21727		0.00528		2.2815		80.2		285.24	
landraces	Water regime (WR)	2	8437858.1	<.001	9699079	<.001	115.1627	<.001	1881.5077	<.001	124398.4	<.001	35741.71	0.003
	Landrace (L)	2	20967029.2	<.001	6773420	<.001	376.3876	<.001	263.9321	<.001	274060.1	<.001	2988.53	0.043
	WR x L	4	108454.5	<.001	4907725	<.001	3.69251	<.001	334.1676	<.001	35337.2	<.001	27006.86	<.001
	WR x Y	2	317.6	0.83	65454	0.001	0.14435	0.263	0.1125	0.93	555.3	0.348	164.6	0.18
	L x Y	2	644.8	0.688	146508	<.001	1.40625	<.001	2.7238	0.198	3590.5	0.005	791.8	0.002
	WR x L x Y	4	5555	0.206	327402	<.001	1.0797	0.005	0.1081	0.997	4318.7	0.012	631.72	0.024
	Pooled error	53	29544991.4		22105917		500.3533		2535.87		450768.3		74657.1	
MNANJE	Year (Y)	1	5073.7	<.001	2693.5	0.013	0.0059	0.841	0.009	0.947	14.03	0.547	165.16	0.12
(Groundnut)	Replication	2	349.1		680.6		0.0792		3.31		22.86		58.21	
	Water regime (WR)	2	566456.4	<.001	3529635	<.001	35.6058	<.001	2107.151	<.001	3785.93	0.001	28043.85	<.001
	WR x Y	2	1711.7	0.021	2947.3	0.03	0.1032	0.7	17.253	0.067	61.2	0.46	622.35	0.035
	Pooled error	17	574681.1		3539207		36.8917		2158.578		4216.45		29656.15	

SOV = Source of variation, D.F. = Degrees of freedom, F pr. = Probability, S.S. = Sum of squares, S1 = Stress during flowering, S2 = Stress during pod development.