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METABOLIC AND PHYSIOLOGICAL TRAITS OF BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA* (L.) VERDC) IN IRRIGATED AND DROUGHT CONDITIONS

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Abstract

Bambara groundnut (*Vigna subterranea* (L.) Verdc) is an underutilised crop grown under rain fed conditions in Africa where drought is a major limiting factor for crop production. Many reports have described Bambara groundnut as a drought resistant crop, however limited evidence exists on the particular extent of resistance and the specific traits and physiological processes that enable it to resist drought relative to other important leguminous crops.

The review paper provides a comprehensive summary of the main lessons learned about Bambara groundnut's drought tolerance, the potential of Bambara groundnut to provide food security in the face of climate change and offers insights for the direction of future research that will allow its potential to be realised in the changing African climate.

The first study was carried out to investigate and gain insights into the physiological responses of two landraces of Bambara groundnut to water stress, including above ground and below ground traits. Plants were grown in PVC columns to allow for sufficient root growth and to ensure a more realistic growing environment. Drought conditions were imposed during late reproductive stages of development. Physiological measurements were taken on site throughout the study with root analysis and yield parameters taken at final harvest. Roots were removed from columns and separated from the stem of the plant before being analysed using root scanning software.

Overall stomatal conductance decreased in both landraces as a result of drought, whereas chlorophyll content showed no signs of decrease. Burkina maintained greater

above ground biomass in both treatments, with higher leaf number, canopy spread, plant height and chlorophyll content throughout, however results suggest this was at the expense of pod production. Nav 4 showed signs of pod formation up to 1 week before Burkina in the irrigated treatment and had significantly more pods under the drought treatment, possibly as a result of its faster development rate allowing it to avoid the onset of drought. Root analysis showed Burkina had a greater surface area and root length in both treatments, with significant longer roots in the drought treatment, possibly allowing it to maintain water availability and ensure above ground plant growth.

The second experiment built on these findings by repeating a similar experiment with larger columns, with drought exposed for a longer period of time and with metabolic assessments. It was expected that drought would lead to a significant change in the characteristics being observed, and that the more drought tolerant landraces would exhibit show a larger root surface area and taproot length and an increase in the biochemical parameters being observed. The hypotheses are shown in greater detail in the following section.

The landrace TVSU89 displayed the highest yield under drought conditions, alongside a reduction in leaf and shoot biomass, higher stomatal conductance and chlorophyll content, reduced root surface area and a greater concentration of anthocyanin. The findings of this work point to further column-based research in more tightly controlled conditions to investigate some of these parameters in more detail.

1. General Introduction

Agricultural production in the 21st century will need to increase not only for the world's rising population, but also to help mitigate the consequences of climate change. The semi-arid tropics of Africa are amongst the most vulnerable regions to the effects of climate change as a result of rising temperatures and changing weather patterns and their impact on rain fed agriculture. A variety of approaches are needed in increasing both the productivity and resilience of farming systems. One such approach from within the scientific community which has been gaining interest and attention is the promotion and development of underutilised crop species. While improving production systems involving the major crops, what is also important is to consider the contribution of indigenous and underutilised crop species. These crops, referred to as 'neglected' or 'minor' crops, are often relatively unimportant in terms of production and economic value but have the potential to contribute food security and improved income (IPGRI, 1999) and have the potential to tolerate various abiotic stresses (Mabhaudi *et al.,* 2016). By increasing diversity in agriculture in this way it not only makes use of valuable plant genetic resource, it also reduces the risk posed by climate change and disease associated with relying on too few crops. An underutilised crop with which substantial work has now been done is the African grain legume Bambara groundnut (*Vigna subterranea* (L.) Verdc). It is grown by women subsistence farmers throughout sub-Sarahan Africa, is highly nutritious, contributes to soil fertility and can be grown on marginal agricultural lands (Mabhaudi *el al.,* 2018). It's reputation as a drought tolerant crop has been well documented and merits further investigation to the specific ways it can contribute to food security in resource poor regions across Africa, particularly those most vulnerable to the effects of climate change.

1.1 Problem statement

Bambara groundnut is a crop with significant potential to contribute to not only the economic development of sub-Saharan Africa, but also to food security and the resilience of communities in the face of a growing climate. In order for this to be realised, however, a thorough understanding of the wide range of traits that enable Bambara groundnut to withstand drought is needed. Further, without this knowledge, true Bambara groundnut varieties that meet the specific needs of different regions and communities will not be able to be developed. The work of this research is yet another contribution to the shared knowledge of this important crop species.

To date, efforts to understand Bambara groundnut represents a unique example of international and collaborative research regarding an underutilised crop species (Azam-Ali *et al*., 2001). Although it has been established that Bambara groundnut is regarded as drought tolerance crop (Mwale *et* al., 2007; Bamshaiye *et al*., 2011; Mazahib *et al*., 2013), the underlying mechanisms are not fully understood. More information is also needed regarding the specific differences in the way different landraces respond to drought. Identifying those processes involved is an essential step towards any possibility of developing superior cultivars of Bambara groundnut. Further, an essential part of this process is thoroughly reviewing the available literature to identify and assess what insights have been acquired thus far and in what direction should research focus.

1.2 Aims and Objectives

The aim of this thesis is to explore and compare the physiological and metabolic traits of selected landraces of Bambara groundnut in irrigated and drought conditions. In particular, this project focuses on the behaviour and characteristics of roots in response to drought as well as above ground physiological processes. In addition, its aim is also to provide a comprehensive review on the literature surrounding Bambara groundnut to aid the direction of and provide insights for future research. The specific objectives are:

- Investigate the effect of drought on the length, surface area, density and fresh and dry weights of roots of landraces of Bambara groundnut
- Investigate the impact of drought on stomatal conductance and chlorophyll content of landraces of Bambara groundnut
- Investigate the effect of drought on development processes, such as leaf number, plant height, canopy spread and final pod yield, on landraces of Bambara groundnut
- Investigate the impact of drought on leaf anthocyanin content in landraces of Bambara groundnut

1.3 Hypotheses

- Drought conditions will significantly affect the growth and development of Bambara groundnut landraces
- Drought conditions will increase rooting depth and accumulation of biomass for all landraces
- Roots under drought conditions will exhibit greater taproot growth

- The more ‘drought tolerant’ landraces from dry climates will demonstrate greater rooting depth and faster rate of development to maturity
- Landraces from wetter climates will progress slower through development stages
- Proline concentrations will be higher in water stressed plants
- Anthocyanin synthesis will increase under drought conditions

1.4 Thesis Structure

This thesis is split into three main parts. The first part represents a published review paper on Bambara groundnut. This paper provides a comprehensive overview of some of the key findings so far regarding the physiological responses of Bambara groundnut. Apart from giving a thorough account of the background to the following two experiments, this paper also proposes possible directions and priorities for future work investigating the drought tolerance of Bambara groundnut.

The second part represents an experiment as a first attempt at adopting a column-based method to assess the response of Bambara groundnut to drought. Focussing on two landraces, this experiment investigated some key above and below grounded traits that may be linked to drought tolerance and evaluated the method of using columns to do so.

Part three of the thesis is a second experiment which took place and sought to build on the findings of the previous trials. Using larger columns and imposing drought for a longer period of time, this second experiment investigate both physiological and metabolic characteristics with potential links to drought resistance.

2 Review Paper

'Bambara groundnut for food security in the changing African Climate'

2.1 Abstract

Global food production must not only respond to the demands of a growing world population, but also to the hazards posed by climate change. Higher temperatures, unpredictable rainfall and weather patterns, changes in growing seasons, increased occurrences of drought and extreme weather events will exert a greater strain on agriculture. Nowhere will these changes have a more detrimental impact than the continent of Africa. It is expected that warming throughout Africa will be greater than the global average, with decreasing precipitation leading to higher occurrence of drought in many regions. Climate change will not only cause shifts in food production and yield loss due to more unpredictable weather patterns, it will also affect food prices and increase malnutrition, especially amongst children. Improving crop productivity and nutritional content in the most vulnerable countries will therefore be vital for mitigating the adverse effects of climate change.

Here the potential of an underutilised crop, Bambara groundnut, to contribute to food security in changing African climates is reviewed. The major points are, 1) Under future climate change scenarios, African rainfall patterns are expected to become more erratic and temperatures will be higher, 2) Climate change predictions in sub-Saharan Africa anticipate cereal yield losses of up to X% in some parts, posing a significant threat to food security, 3) With only three plant species accounting for more than 90% of the world's caloric intake, it is clear that an abundance of genetic

resources and potentially beneficial crops are being neglected, 4) There is now ample evidence demonstrating Bambara groundnut's superior tolerance to drought conditions relative to other legumes, 5) Bambara groundnut has a high nutritive content and can therefore be used in combatting malnutrition, 6) Bambara groundnut can be successfully intercropped with African staple cereals to improve productivity and contribute to soil fertility through nitrogen fixation. It is hoped that this review will bring attention to this important legume and increase awareness of its potential.

2.3 Introduction

One of the greatest challenges facing humanity in the 21st century is ensuring global food security in a changing global climate. Limited land availability, unprecedented population growth along with urbanisation are issues which agriculture must now confront in the face of changing global climate. In its most recent report, the United Nations-sponsored Intergovernmental Panel on Climate Change (IPCC) predicts with greater confidence that climate change will have adverse effects on food security in many parts of world, particularly the most vulnerable developing countries (IPCC, 2014). In particular, climate change poses a threat to one of humanity's most vital natural resources: freshwater. Changing precipitation patterns and other variables are expected to reduce water supply in many areas across the world, resulting in depleting water resources for agriculture and rising water insecurity (Hagemann *et al.,* 2013). These changes will put a significant strain on already fragile food systems and stretch even further the resources needed to ensure food security. While it is expected some regions will benefit in the short term from rising temperatures in terms of crop yields, the majority of the world's poorest and least prepared populations will become increasingly vulnerable to food insecurity.

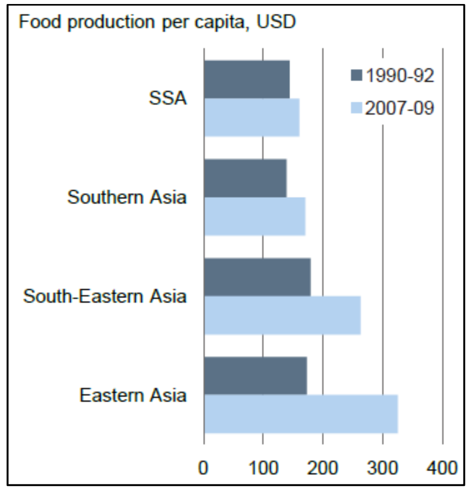


Figure 1: Food Production per capita (USD)

Despite economic growth in many Africa countries, food production has remained underdeveloped and amongst the lowest in the world. Source: Schaffnit-Chatterjee (2014).

It is expected that rain-fed agricultural systems in the tropics, which are among the most susceptible regions to climate change, will experience the most severe effects (Calzadilla *et al.,* 2009). Further drying of semi-arid regions is anticipated, leading to increasing drought conditions which will create challenges for water management. Coincidentally, it is also these regions which from a geographical viewpoint represent some of the world's poorest populations, particularly many countries across semi-arid Africa. With low income potential and adaptive capacity and already widespread poverty, climate change has the ability to impair and even reverse socioeconomic progress made in recent years in sub-tropical Africa (Ford *et al*., 2014). As rainfall patterns become more unpredictable, drought conditions will become more prevalent and yields of the most important food crops such as maize (*Zea mays*), rice (*Oryza* spp) will be threatened. In addition, changing weather patterns and increases in extreme weather events will have consequences not only for agricultural productivity but also for the cost and affordability of food (FAO, 2013; Lobell and Field, 2007). However, it is an unfortunate paradox that while Africa comprises some of the world's poorest and most vulnerable communities to climate-linked food insecurity, it also represents vast regions of untapped fertile and agricultural land with more than 200 million hectares yet uncultivated; almost half of the global availability (Chamberlin *et a.,* 2014). Unlocking the potential of Africa's land and resources could significantly boost productivity, improve incomes and increase agricultural exports (Schaffnit-Chatterjee, 2014).

Rising global temperatures and changing weather patterns will alter ecosystems and exert new pressures onto the planet's plant and animal species, including those used for agricultural production. As the climate changes, so do the environmental conditions in which the world's most important food crops grow, potentially making them less resilient and productive. In some cases climatic conditions may change too rapidly for many plant species to adapt (Botero *et al*., 2015). While these changes will have consequences globally, few countries will be affected more acutely than those in the semi-arid regions of Africa.

2.3 Climate change in Semi-arid Africa

Africa is often cited as the continent most vulnerable to the negative consequences of climate change as up to 95% of farmed land is rain fed and agriculture represents the main livelihood for the vast majority of the rural poor (CABI, 2009; Boko *et al.,* 2007). Further, of the 32 countries in the world facing food crises and requiring international emergency support, 20 of them are in Africa (FAO, 2013). For such countries, agriculture is a significant if not the most significant aspect of the economy. In Malawi for example, 40% of the country's GDP comes from agriculture and is a source of employment for three quarters of the population (IFPRI 2012). Similarly agriculture contributes around 35% towards GDP in Ghana (Jerven and Duncan, 2012) whereas in Ethiopia it is as high as 45% (Tilahun *et al.*, 2011). While the challenges of climate change are global, poor infrastructure and a weak capacity to adapt to new threats and sudden changes pose a significant threat for Africa's poorest nations and its people (UNDP, 2012).

The second half of the 20th century saw a number of food crises throughout Africa which were at least partially the result of extreme weather events. One of the most severe cases in the last 30 years was the 1983-1985 famine in Ethiopia which resulted in more than 400,000 deaths. Although it is believed that government policy and civil war were amongst the underlying causes, drought is regarded as a confounding factor that further exacerbated the crisis. (IFPRI, 2012). In 2005 Malawi experienced a more than 60% drop in maize (*Zea mays*) yields as a direct result of drought, affecting more than 5 million people and requiring international aid (FAO, 2005; Devereux, 2002). More recently, tens of thousands died from starvation in 2011 throughout the Horn of Africa following severe drought and failed harvests (OCHA, 2011). In 2012 severe drought hit the Sahel region, resulting in acute food insecurity with millions today still facing a deteriorating outlook (FAO, 2014). Substantial and continuous humanitarian support is needed across the Sahel for the more than 20 million affected, for which the UN has released an urgent international appeal for more than US $2 billion and has developed a regional 3-year strategy to support vulnerable populations (OCHA, 2014). As well drought, heat stress events present another major threat to food security in the sub-Saharan region and will become more frequent in tropical regions (Olsson *et al*., 2014; Fischer et al., 2005). Battistic and Naylor (2009) predicted that hot spots for heat stress will occur across the Sahel and East Africa, affecting Maize yields in particular. The nature and frequency of such events will be a major factor in determining future climates in sub-tropical Africa.

It is clear that the adverse effects of climate change pose a significant risk to the vulnerable populations in semi-arid Africa. While some progress has been made towards reducing hunger in these countries, large populations still depend on rain fed agriculture for their livelihoods, resulting in high levels of vulnerability to increasing extreme weather events such as drought (Shongwe *et al.*, 2011; Lyon and DeWitt, 2012). The nature of the predicted changes will now be explored in more detail.

2.4 Rainfall patterns

As the planet's surface temperature rises, overall there is a two-fold effect on global rainfall patterns. On the one hand, the moisture holding capacity of the atmosphere increases as the warmer air can retain more water, while on the other, increased temperatures lead to more evaporation (Houghton *et al*., 2001). This both adds water to the atmosphere and increases rainfall, but also removes water from oceans, rivers and arable land and increases salinization of soils (Várallyay, 2010). In sub-Saharan Africa, the general trend is that rainy seasons are expected to become wetter, while the dry season becomes drier. Rainfall projections by various intermediate climate change models vary, but at this stage there is some agreement that rainfall will increase in some parts, including East Africa, while Sahelian and Southern Africa are likely to experience decreased rainfall and shorter rainy seasons (James and Washington, 2013; Shongwe *et al*., 2011). Further, reports mention that there has been a continued warming in the Indian-Pacific pacific region over the past 30 years which has contributed to increasing occurrences of droughts in East Africa(Williams *et al*., 2012). At the same time, heavy precipitation during the rainy season will become more common which can potentially lead to flooding and soil erosion. Hulme *et al*.,(2001) suggest that by 2050 East Africa will be faced with up to 20% increase in rainfall from December – February and a 5-10% decrease in rainfall from June to August. Seneviratne *et al.*, (2012) suggested with high certainty that the number of extreme wet days in the same region has and will continue to increase. However, not only is it likely that the increase in rainfall will be more sporadic and unpredictable and therefore difficult to manage, it may well be the case that rainfall comes in the form of intermittent and heavy rainstorms. Heavier rainfall is also expected to contribute to soil erosion and consequently loss of soil fertility due to nutrients lost from the topsoil (Lal *et al.,*2011; Bates *et al.,* 2008), requiring new management practices, especially at the farm level, to mitigate these effects and ensure soil conservation.

Combined with a decrease in rainfall during the already dry season, countries such as Kenya will be faced with complicated water management issues and the need to adopt sustainable methods for maintaining food production. River systems which are a vital source of water for many populations will be affected by these changes. Bordering Kenya, the basin of the River Pangani of Tanzania is expected to experience a similar increase in rainfall during the wet season (November – March) and a decrease during the dry season (June – October), with increased evapotranspiration expected towards the end of the dry season (IUCN, 2011). This is projected to result in a 6-9% reduction in annual flow, adding further pressure to the demand for water along the river which provides agricultural irrigation for an estimated 55,000 hectares of land and is a source of livelihood for over three million people (IUNC, 2011). Reduced stream flow will become a more common reality for numerous river systems across Africa, particularly in the southern regions, where most studies suggest reductions of up to 50% will be seen by 2050 (Kusangaya *et al*., 2014).

While indications of increasing precipitation suggests a hopeful future, the reality is that water shortages are still occurring and water will become increasingly scarce in the long term with increasing urbanisation and competition for water resources (Druyan 2011). Any increase in rainfall during the rainy season is likely to be more extreme and unpredictable, whilst countries along the Sahel and southern arid countries such as Tanzania, are likely to experience lower rainfall and reduced river flow. Should rainfall follow this pattern of becoming more extreme and erratic, adaptation and mitigation strategies will need to be adopted urgently to optimise water resources for the most susceptible regions.

2.5 Rising Temperatures

In addition to changing rainfall patterns, rising temperatures poses a significant threat to rain fed agriculture as a result of increased evaporation, changes in soil moisture and groundwater reserves and increases in the frequency of droughts (Schulze, 2011). Warming is expected to be higher than the global mean for all seasons across Africa, with the already rain dependent semi-arid regions facing the most vulnerability (Kusangaya *et al*., 2014). Mean annual temperature rise across Africa is likely to exceed 2°C by 2100, with southern Africa, East Africa and the Sahel experiencing the most warming (Kruger *et al.,* 2004). According to Battisti (2009), there is a high probability (greater than 90%) that by the end of the 21st Century, average growing season temperature in the tropics and subtropics will be higher than the highest seasonal temperatures seen from 1900 to 2006.

This increase in temperature will certainly negate any increase in rainfall, as more water will be lost through evaporation, further exacerbating the dry season (James and Washington, 2013). Additional loss of water through evaporation will put an even greater strain on water management, and by 2080 there will be more arid and semi-arid land across Sahelian Africa and an increase in desertification as a result (James and Washington, 2013; Nikulin 2012). For those regions receiving less precipitation, a hotter climate will put an even greater strain on the already dry soils and further constrict water availability. East Africa, for example, is expected to continue to experience drought events at seven-year intervals, but will be more extreme and hard hitting as water becomes even scarcer during the dry season (Boko *et al.,* 2007).

2.6 Impact on Food Security

Inevitably these changing climatic conditions will impact crop production across the sub-Saharan region, with cereal yields facing a significant risk. A review by Zinyengere *et al*., (2013) consolidated the findings of various climate change impact studies in southern Africa from 2001 to 2011. While variation and discrepancies were found to exist across different models, it was concluded that the overall impact of climate change on crops in sub-Saharan Africa will be negative. This correlates with other studies which suggest negative impacts of climate change on crop production (Liu *et al*., 2013; Muller, 2013).

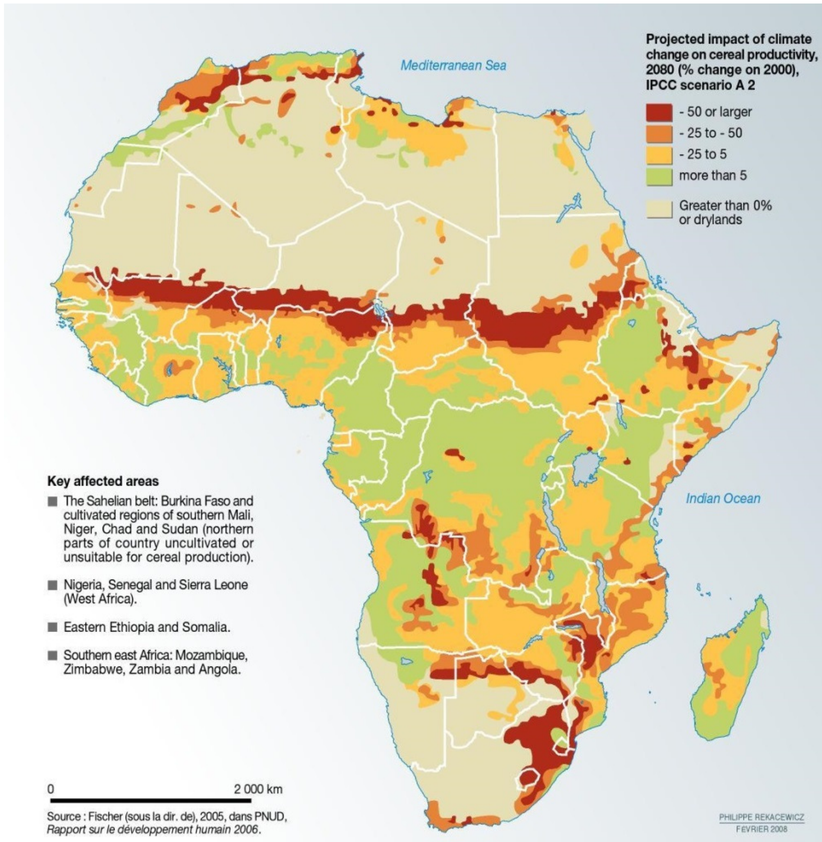


Figure 2: Impact of climate change on African cereal production (Fischer *et al*., 2005)

Changes in cereal production vary greatly, however those regions along the Sahelian belt and the semi-arid countries to the south are at the greatest risk.

Maize is one of the dominant crops in Zambia, Tanzania, Kenya, Ethiopia and Nigeria, with wheat (Triticum spp), rice (Oryza sativa), sorghum (Sorghum bicolor (L.)) and millet (*Pennisetum* glaucum) also having important roles in calorific intake (IFPRI, 2012; Romney et al., 2003). While the latter two may display higher yields in some areas due to their higher tolerance of heat and water stress, projections indicate that most cereal crops across semi-arid Africa will face yield losses (Waha *et al*., 2013).

Yield losses will drive food prices higher, resulting in unaffordable food prices and therefore a greater a risk of malnutrition (FAO, 2008; Holden, 2009).

Results obtained by Knox *et al*., (2002), one of the few studies to provide evidence for the impact of climate change on Africa's major crops, identified consistent yield loss of wheat, maize, sorghum and millet by the 2050s. In a later study, Knox *et al.,* (2010) incorporated irrigation and water resources into their analysis of how rising temperatures will affect sugarcane (*Saccharum officinarum*) yields in Swaziland. It was concluded that in order to only maintain current yields, irrigation would need to increase by more than 20%. Schlenker and Lobell (2010) proposed that aggregate production changes in maize, sorghum, millet, groundnut and cassava is likely to exceed 7 percent and in certain scenarios could reach as high as 27%, while Berg *et* al., (2013) projected that even yields of C4 species, such as millet, will decrease by an average 6 percent. In fact for the grains alone, Lobell *et al.,* (2012) estimated that for each degree Celsius temperature rise, global yield loss is approximately 5 percent. At the regional level, however, the impacts vary. While some regions will experience an expansion in the areas suitable for growing cereals, this will be negated by the loss of land as a result of increased heat stress in others. For the arid and semi-arid zones, precipitation changes are likely to be the main driver behind yield losses (Berg *et al*., 2013). In Southern Africa, even moderate temperature increases may lead to significant yield loss. Maize, the staple crop of the region, may face yield reductions of up to 30% by 2030 if temperature rises along its expected trajectory (Lobell *et al*.,2008; Easterling *et al*.,2007).

Global prices of maize, rice and wheat are projected to increase by 4, 7 and 15 percent respectively by 2050 as a result of climate change-linked yield loss, in addition to other important crops such as cassava, millet and sorghum which will see price increases of 20, 5 and 4 percent respectively (IFPRI, 2011). Such an rise in cost will cut the affordability of the most important crops for human consumption and livestock feed, leading to an expected drop of calorie availability of 37 kilocalories per capita per day across SSA, with the central zone being hardest hit (IFPRI, 2011). Figure 3.0 below summarises the main impacts of drought that would affect smallholder farming systems across Africa.

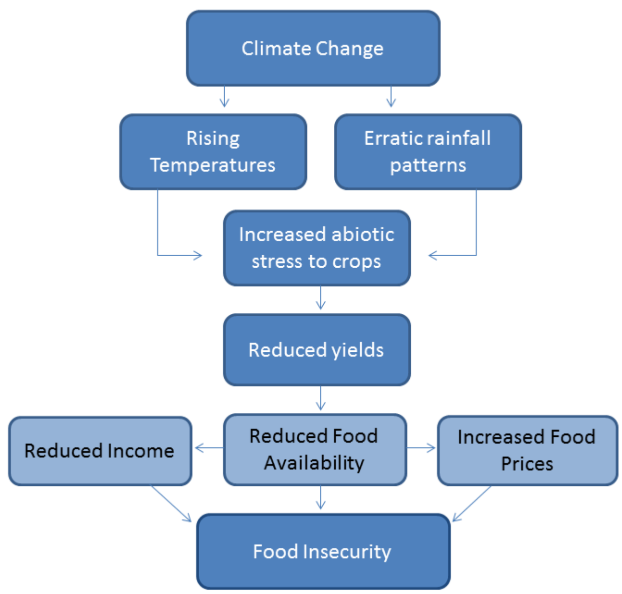


Figure 3: Impacts of drought, adapted from Gitz and Meybeck (2012).

Environmental stresses increase the risk of food security not only through yield losses, but also through reducing income and pushing up food prices. In regions where widespread poverty is prevalent, drought conditions will have increasingly severe social, economic and environmental consequences.

2.7 Solutions

It is clear that the primary impact of climate change throughout Africa will relate to water availability, management of water resources and nutritional security, as has been highlighted by the United Nations (UN-Water, 2010). Although the precise way in which weather systems will change is not clear for all regions, what is expected is that climate change will cause shifts in cereal growing areas and increase the risk of crop failure due to intensified drought and heat stress. This in turn will increase food prices and therefore lower the affordability of basic staple foods and animal feed for those most vulnerable, further exacerbating malnutrition, especially amongst children (Ringler *et al*., 2010).

It follows then, that any effort to mitigate the consequences of climate change must explore ways to improve the resilience of farming systems to water and heat stress, particularly those that are rain-fed (Ros*t et al*., 2009). Doing so will help to increase food availability and improve rural incomes, thereby negating the consequences of dropping yields and rising food prices.

One strategy that has been advocated is the development of superior varieties of important cereal crops, enhancing drought resistance or nutritive content through genetic modification or other breeding technologies (Najafi and Lee, 2014; Qaim, 2011). While such an approach will no doubt be of great importance in improving incomes and ensuring food security in more hostile African climates, it can be argued that what is more pressing is a fundamental restructuring of the way Africa grows and distributes food (UNDP, 2012). Poor infrastructure, political instability, limited access to technology and education and financial constraints are amongst the many hurdles that would make difficult the introduction of high yielding varieties of the major crops. The Green Revolution, which was so successful in South and East Asia, has so far not reaped the same benefits in sub-Saharan Africa. This has been the result of a combination of factors including poor infrastructure in many African nations, unfavourable environmental (including irregular rainfall and soil properties) and the high cost of the technologies and inputs involved (Lynd and Woods, 2011; Diao *et al*., 2010). This is perhaps an indication that high input, mechanised agriculture is unlikely to provide the necessary solutions for the resource poor farmers in semi-arid Africa, especially in the face of climate change (Frankema, 2014).

Food systems and crops that can withstand the shocks of increasingly hostile climates will be better suited to protecting livelihoods, yet many modern varieties of the major crops are vulnerable to heat and drought stresses (Lobell, 2012).

An approach that is likely to prove more relevant and sustainable for the arid regions of Africa, is the exploitation of minor and underutilised crops, especially species native to the continent of Africa. Crops that have evolved and been cultivated in Africa's various climatic conditions are likely to grow more favourably in African climates and will contain characteristics and traits that enable them to withstand abiotic stresses and unfavourable conditions (Sambo, 2014). Tapping into these local resources is vital for building resilience in rural communities and their farming systems.

2.7.1 Underutilised Crops

Underutilised crops, also known as 'neglected', 'minor' and 'orphan' crops, are those species which are of little importance globally in terms of production, consumption and economic value but have great potential to contribute to food security, improved income and nutrition or may be of medicinal use (IPGRI, 1999). Such species are considered underutilised as they have not been given the necessary support either by research, policies or legislation that would enable them to make such contributions. They are often regarded as traditional crops and are usually found in a specific region or ecological niche and represent an untapped source of agrobiodiversity. Many of these species have been grown locally for centuries and appear to have been chosen due to their ability to tolerate unfavourable environments (Azam-Ali *et al.,* 2001). These crops represent a wide range of species, including cereals: finger millet (*Elusine coracana*) and Teff (*Eragrostis tef),* fruit species: jackfruit (*Artocarpus heterophyllus*), legumes: Bambara groundnut (*Vigna subterranea* (L.) Verdc), the azuki bean *(Vigna angularis*), root crops: African Yam bean (*Sphenostylus stenocarpa*), and many others (FAO, 2013).

In the effort to combat climate-related challenges, issues relating to food distribution, sustainable livelihoods as well as socio-economics are necessary areas of intensified focus and development (Connolly-Boutin and Smit, 2015). However, tapping into a wider genetic pool of potentially beneficial agronomic traits and characteristics will increase the resilience and adaptability of agriculture to changing climates. Indeed, José Graziano da Silva, the Director General of the FAO, stated at the International Crops for the 21st Century Seminar in 2012 that underutilised crop species "play a crucial role in the fight against hunger and are a key resource for agriculture and rural development" (FAO, 2012). In recent years, the subject has started to attract more attention from research institutions, organisations and governments as the importance of agro-biodiversity becomes more recognised (HLPE 2012; Gowda 2007).

This new interest in agro-biodiversity has emerged from an increasing awareness of the risks associated with relying on too few crops and the vast untapped potential of the world's plant resources. Only 30 crop species provide 95% of the world's food, with maize, wheat and rice providing more than half of the world's calorific needs despite more than 7,000 cultivated species being known to exist (FAO, 1996). This state in which global agriculture finds itself not only deprives humanity of a vast reservoir of plant resources, but it also gives rise to many risks that are associated with relying on just a handful of species. The increasingly global and interconnected nature of agriculture means that any setbacks in production will have far reaching consequences, for both people and economies.

Diseases and pests pose a particular threat. If a serious outbreak of a particular pathogen occurred amongst any of the world's major crop species, food prices would escalate and food shortages will become widespread, leading to large scale food crises. Such a possibility exists with the fungus *Puccinia graminis tritici* strain known as UG99, which causes stem or black rust disease in wheat. First detected in Uganda in 1999, several races of the same lineage have already spread to Zimbabwe, South Africa, Sudan and Yemen, and in 2007 the disease was found to have reached Iran (Singh *et al.,* 2011). This particular strain produces devastating yield losses of up to 70 to 100 percent if preventive measures are not taken, and it is feared that spores will continue to travel by wind to India, which is second largest producer of wheat in the world (FAO, 2010). While efforts are underway to prevent an outbreak by identifying resistant wheat varieties, the situation highlights the susceptibility of agricultural systems characterised by low crop and genetic diversity.

Similarly, as the future climate across Africa will become increasingly characterised by drought, rising temperatures and erratic rainfall patterns, any susceptibility amongst the staple crops will affect millions of people. Economically, global food prices are delicately linked to crop production and the fluctuating costs of commodities, such as oil. The risk associated with this scenario is perhaps demonstrated most clearly with rice: it is the staple food for more than three billion people and in 2008 when the cost of rice increased threefold, more than 100 million people were pushed into poverty (IRRI, 2011).

As climate change intensifies drought conditions, countries affected by political instability are likely to become more vulnerable to poverty, as food and water shortages along with rising prices exacerbate existing economic and socio-political tensions (Smith and Vivekananda, 2007). Dependence on rain-fed agriculture and the fragility of political and social infrastructure in many countries makes African agriculture especially vulnerable to further food crises (Knox, 2012).

While enhancing the institutional and administrative capacity of nations to adapt to these tensions is vital, ensuring food security for those most vulnerable is no less essential, and the 'cornerstone' of any strategy to achieve food security in the world's poorest countries is, as reiterated by the FAO, the expansion and diversification of food production (FAO, 2008).

Many different species around the world have been identified as underutilised and with potential to contribute to food security in their respective regions. The relative success of a Quinoa (*Chenopodium quinoa*) for example, demonstrates the potential for indigenous crops with nutritional benefits to contribute to food production globally (Ruiz, *et al*., 2014). Such crop plants represent a cross section of the planets' plant diversity.

One crop group which is of major agricultural important across sub-Saharan Africa and contains species with potential to contribute to improved incomes, nutritional security and food production are the leguminous crops (family *Facaceae*) (Sprent *et al*., 2010). Legumes represent almost 18,000 species and include widely grown food crops such as cowpea (*Vigna unguiculata*) pigeonpea (*Cajanus cajan*), common bean (*Phaseolus vulgaris*) and groundnut (Arachis hypogae) (Graham and Vance, 2003). Many species are grown in intercropping systems throughout sub-Saharan Africa where they appear to offer protective control for Sorghum and Maize against pests such as *Striga hermonthica (Khan et al., 2007).* The protein-rich food which legumes offer, as well as the ability for many species to contribute to soil fertility through nitrogen fixing symbioses, makes them important components of any future cropping system (Jensen *et al*., 2011).

As well as improving food security through increased food production, it is also essential to improve the resilience of farming systems to withstand the pressures of climate change. Leguminous species, through their agroecological benefits and many end uses, are examples of untapped plant resources that could be used to improve the productivity and adaptability of food systems in the most resource poor regions of Africa.

Amongst this family is Bambara groundnut (*Vigna subterranea* L.); an African grain legume that has received interest in recent years for its tolerance to drought conditions and its potential to contribute to food security, particularly on its home continent. The next sections will now explore the literature on some of the physiological traits of Bambara groundnut that make it a suitable candidate as a food security crop in changing African climates.

2.8 Bambara groundnut

Since 1988, Bambara groundnut research has steadily increased and has involved international collaboration between various Universities and institutions (Dakora, 1998; Amarteifio and Moholo, 1998). The result today is a comprehensive body of knowledge about the crop covering genetic diversity, drought resistance and adaptation, nitrogen fixation and intercropping and other physiological and molecular aspects, some of which will be explored in this review. In addition to the gained scientific knowledge, the potential of the crop with regard to market, economy and diet has been considered. This is especially important for many underutilised crops whose acceptance and increased production is limited by poor markets (Mayes *et al.,* 2011). The history of Bambara groundnut research represents a unique case study of how work on underutilised crops can take place (Azam-Ali *et al*., 2001).

According to Doku and Karikari (1971) bambara groundnut has two botanical forms; the wild type (var. *spontanea*) and the cultivated forms (var. *subterranea*) which originated from the former through gradual changes. The landraces have developed as a result of selections made by farmers based on their traits which make them reliable in various climatic conditions (Doku and Karikari, 1971; Massawe et al., 2005).

Image 1.0: Bambara groundnut seeds and plant morphology

Great diversity of seed colour exists between landraces. As with many legumes, Bambara groundnut leaves are trifoliate and seeds develop in pod fruits, either above or below ground, as seen on the image on the right. Images taken from the University of Nottingham (www.nottingham.ac.uk).

Its centre of origin is believed to stretch from the Yola region of Nigeria down to northern Cameroon and is now cultivated throughout the African continent, South-east Asia and South and Central America (Azam-Ali, 2001; Hepper, 1963). Currently regarded as an underutilised crop, it is grown mainly by resource poor women subsistence farmers in sub Saharan Africa. It is regarded as a complete food with many different uses in different regions (Bamshaiye *et al.*, 2011). Its seeds can be eaten fresh, used to make flour, can be pounded or ground into a stew and is often cooked to be consumed with rice and in traditional dishes ,while in some countries the seeds and plant are used for livestock (Linnemann and Azam-Ali, 1993). In Burkina Faso, for example, the protein and phosphorus-rich leaves are often used for fodder and in

Botswana the stems are used for grazing (Bamshaiye *et al.,* 2011). As is characteristic of many underutilised crops, Bambara groundnut is currently cultivated from landraces as varieties with specific traits are yet to be developed.

2.8.1 Production and Importance

Bambara groundnut is grown throughout the tropical regions of Africa and in 2009 the largest producer was Burkina Faso, with around 44,000 tons harvested, and followed by Cameroon, Democratic Republic of the Congo and Mali (FAOSTAT, 2011). Global production in 2009 was just over 100,000 tons (FAOSTAT, 2011).

Although compared to major crop species there has been limited research attention, enough has been found to demonstrate that Bambara groundnut has certain advantages over other legumes and indeed other crops. Experimental studies have shown, for example, its superior drought tolerance and nutritive content relative to other legumes (Bamshaiye *et al*., 2011; Mazahib *et al*., 2013). Despite its beneficial traits, barriers to wider acceptance exist. Although in some areas there is rising interest in the crop, the popularity and familiarity of other cash crops such as soybean make them a financially safer option (Mkandawire, 2007). Its reputation as a snack or food supplement means its status is low and is not considered as a crop with economic value (Azam-Ali *et al.,* 2001) and in some parts has obtained the unfortunate byname of a 'poor man's crop' (Heller, 1997;). There is no doubt however that this crop deserves more recognition. Through education, support from policy makers, scientific research and initiatives by governments, Bambara groundnut's potential can be more fully realised.

Under ideal conditions and with appropriate management yields up to 4000 kg/ha have been observed (Heller *et al.*, 1997) and it has been suggested that there is potential for wider cultivation and higher yields than what is currently achieved in sub-Saharan Africa (Azam-Ali et al. 2001).

Known in Madagascar as 'a seed that satisfies', it is highly nutritious with high protein and carbohydrate content (Azam-Ali *et al.,* 2001). Work has shown that Bambara groundnut is a richer source of protein (16-25%) than cowpea, groundnut and pigeon pea (Brough *et al.,* 1993; Brough and Azam-Ali, 1992; Poulter and Caygill, 1980). Starch content is also favourable at 43% and lipid content (7.9%) exceeds that of cowpea (1.0-1.6%) and pigeon pea (1.2-1.5%) but not groundnut (45.3-47.7%) (Brough and Azam-Ali, 1992). In the case of Bambara groundnut, it is a strange paradox that such a nutritionally whole plant that can significantly contribute to alleviating malnutrition should be so neglected and overlooked in its homeland.

A more detailed look will now be given to what qualifies Bambara groundnut as a potential food security crop in the sorts of conditions that will increasingly characterise many regions across Africa in the next 50 to 100 years.

2.8.2 Bambara groundnut Tolerance to Water and Heat Stress

With the changes in weather and rainfall patterns expected to occur across semi-arid Africa, it is essential to grow crops that can ensure reliability during unpredictable climatic conditions. In the tropics soil moisture is the primary limiting factor to yield and crop production and will continue to exert more pressure with increasing temperatures and changing rainfall patterns. For many African countries in the tropics, irrigation and adequate water supply for agriculture presents a long term challenge (UNDP, 2012).

There is now strong evidence that Bambara groundnut is more drought tolerant than many of its legume counterparts (Babiker, 1989; Collinson *et al.,* 1996; Vuragai *et* al., 2011; Berchie *et* al., 2012) Early work indicated the drought tolerance capacity of Bamabra groundnut (Doku and Karikari 1971), however it has only been in the past few decades efforts have been made to understand and quantify how periods of drought are tolerated.

Plants that grow in areas where water is the major limiting factor have evolved various means of ensuring their growth and development in times of water stress. Turner (1979), in a discussion of the physiological aspects of drought tolerance, suggested that there are three main mechanisms by which plants cope with periods of water stress. These three mechanisms are known as 'drought escape', 'drought avoidance' and 'drought tolerance'. The first of these is usually a short-term strategy whereby the life cycle of a plant is completed before periods of drought. 'Drought avoidance' involves physiological changes, such as reducing leaf expansion, promoting root growth or reducing stomatal conductance and can be seen in sorghum and cowpea (Osonubi, 1985; Stout and Simpson, 1978) as well as Bambara groundnut (Collinson *et al*., 1997). Finally, 'drought tolerance' is linked with survival strategies which are used in severe drought conditions and is less relevant to agriculture. The lack of quantitative evidence available means that it has not been possible to easily place Bambara groundnut into only one of these categories and instead elements of each have been observed in landraces Jørgensen *et al*., (2010).

Indeed, great intraspecific diversity exists in terms of how well plants cope with drought. For example, the landrace known as UNISWA red from Swaziland is regarded as having a relatively low tolerance compared to S19-3, a very drought tolerant landrace from Namibia Jørgensen *et al*., (2011). In addition, molecular and genetic analyses have confirmed the great diversity that exists between landraces (Amadou *et al.,* 2001; Massawe *et al.,* 2002; Molosiwa *et* al., 2013; Mukakalisa *et* al., 2013; Siise and Massawe, 2013;). Such diversity demonstrates the vast pool of genetic resources that can be used in future breeding efforts.

Collinson *et al.,* (1997) and Colllinson (1996) and both assessed the response of Bambara groundnut under different irrigation treatments. Collinson *et al.,* (1996) observed that water stress resulted in reduced leaf initiation rates, leaf and pod number per plant, dry matter, leaf area index and the efficiency of conversion of intercepted radiation into dry matter. Interestingly, the treatment which received no further irrigation at all from 35 DAS was still able to produce some pod yield, albeit very low (0.1 t ha $^{-1}$). This contrasts with previous work carried out on groundnut under similar conditions in which it was unable to produce any pods (Babiker, 1989). Importantly, what this study identified were some plant responses that seem to have a role in tolerating drought, namely an economical way of using available water such as by a reduction in leaf area development and an increased partitioning of dry matter to the roots, as well as increasing root density. The later study, Collinson *et al.,* (1997) built on these findings by identifying other apparent adjustments made by the crop. Water potential was maintained during water stress and was associated primarily with a combination of stomatal regulation, osmotic adjustment and reducing leaf area index.

Experimental evidence demonstrates that much potential exists amongst Bambara groundnut for climatic adaptation and that great diversity exists in the ways landraces respond to different environmental conditions. Twin publications by Mwale *et al.,* (2007a and 2007b) looked at the effect of water stress on different aspects of the crops' growth and development. One focused on the impact on dry matter production and yield, while the other explored resource capture and conversion. Both confirmed previous work showing that much variation exists between landraces in terms of responses to drought, as a result of the different environments from which they originated. A plant originating from an environment characterised by low mean annual rainfall and a short growing season is likely to have a relatively short life cycle. On the other hand, a longer life cycle would be permitted in a climate with higher rainfall and a longer growing season. Such differences are reflected in the data. For example, the landrace S19-3, which is from the first of these two climates (Namibia), displayed a better performance under the drought treatment than DipC and Uniswa-red, which are from the latter (Botswana and Swaziland respectively). This is a result of its faster growth and development rate, its early maturity, and also relatively more efficient use of water, as has been confirmed in other studies (Karunaratne, 2009; Karunaratne *et al*., 2010; Jorgensen et al., 2011). Landraces such as S19-3 would be more advantageous where terminal drought is a problem, due to their shorter pod filling periods. Where the growing season is not a limiting factor or where rainfall is more uniformly distributed, Uniswa red would produce higher yields due to its longer life cycle. Findings such as these are essential as they demonstrate the most suitable conditions for a certain landrace and can help inform crop management in changing weather patterns. Further, such variation can be harnessed for selections in breeding programmes that can develop true varieties of the crop that are adapted to and high yielding in future climates across Africa.

In the second of the two studies by Mwale *et* al., (2007), an average seed yield of 1.65 t ha^{-1} was achieved which is higher than reported yields from cowpea (0.3-0.5 t ha^{-1}) under similar conditions (Leport et al., 1999). Similarly across all landraces was a reduction in the mean fractional intercepted radiation (f) during drought, which was reduced from 0.8 to less than 0.7. Seasonal intercepted radiation was also hindered, which is consistent with the findings of Collinson et al., (1999). An interesting outcome of this work was the observation that those plants in the irrigated treatment extracted water from the top 50cm of the soil, while the roots of those experiencing drought were found throughout the soil profile, some reaching as far as 90cm.

An aspect of Bambara groundnut physiology studies that was until recently not fully considered was the relationship between the mechanisms underlying drought tolerance and the final crop yield. This was recently explored by Jørgensen *et al*., (2011) who imposed drought on four landraces during the early reproductive stage. Stomatal response and transpiration were investigated as with previous studies, however the effects of these on yield components were considered. While there were similarities amongst the landraces in terms of stomatal response, variation could be seen in seed yield reduction and the effect on yield components and cumulative plant water use. Seed yield loss was greater in LunT (from Sierre Leone) and Ramayana

(Indonesia) compared to Uniswa-red and S19-3 and the former two also had fewer larger seeds than the latter. LunT and Ramayana are therefore more sensitive to drought than the other two landraces. Again, these responses reflect the adaptations the landraces have developed in response to their local climates. An interesting finding was that the fraction of transpirable soil water (FTSW), while similar among the landraces, was much higher than those identified in other crops (Sadras and Milroy, 1996). This may suggest that Bambara groundnut possesses a greater sensitivity to water stress and soil drying than other crops.

As African climates will get hotter as well as generally drier, selection of crops for use in these environments must consider both of these factors. Limited research has been done to identify the response of Bambara groundnut genotypes specifically to temperature stress, but those that have revealed useful initial insights. Berchie *et al.,* (2012) evaluated the response 5 landraces of Bambara groundnut to temperatures ranging from 34.7 to 38.7 °C. As temperatures exceeding 38°C, pod yield was negatively affected even though irrigation was provided. Nevertheless, the landrace Burkina, from Burkina Faso, proved to be the most drought tolerant landrace and still managed to produce pods at high temperatures whilst other landraces produced none. Likewise, Shareef *et al*., (2014) found that during high temperatures and under moderate drought, the landrace S19-3 produced significantly higher pod yields than Uniswa Red. Further, results suggested that water stress produces a greater response in crops compared to temperature stress; an indication that plants in the tropics may be better suited to tolerate high temperatures alone. Although both studies demonstrate that traits linked with heat tolerance exist amongst genotypes, more experiment research is needed in this area to produce more valuable insights into the potential of Bambara groundnut in hotter climates.

2.8.3 Potential of Bambara groundnut as an Intercrop

Any climate smart strategy to ensure food production must include sustainable soil management practices. Further, such an approach will also need to consider the fact that most farmers across semi-arid Africa are not sufficiently equipped with the technological or financial means of applying modern, conventional farm management techniques designed for monocultures (UNDP, 2012). Intercropping and agroforestry are common practices throughout Africa and have already proved to be useful means of improving utilisation of plant resources, reducing soil compaction and at the same time improve yields whilst maintaining soil fertility and health (Khan *et al*., 2014; FAO 2012; Scherr *et al.,* 2011).

Nitrogen fixation makes legumes valuable crops in low-input agriculture where nitrogen fertilizer is rarely used. Bambara groundnut is usually intercropped with cereals and root crops, namely maize*,* cowpea, sorghum*,* pearl millet and peanut (*Arachis hypogaea*) and is frequently used in crop rotations (Ntundu, 1997; Mukurumbira 1985). Studies exploring the nodulation capacity of the crop have found that Bambara groundnut's nitrogen requirement is met by nitrogen fixation and compares favourably against other legumes (Somasegaran *et al*., 1990; Doku 1969). Investigations into the crop's nitrogen requirements have also shown that while nitrogen fertiliser increases vegetative growth, there is relatively little gain in terms of yield development (Adjetey and Sey, 1998). A deeper understanding of this process in landraces of Bambara groundnut is needed as those which are superior in fixing nitrogen may be potential sources of genetic variation for producing improved cultivars.

Kishinevsky *et al.,* (1996) studied the nodulation and nitrogen fixation of 23 Bambara groundnut landraces from Malawi. Two strains of *Bradyrhizobium* (100M and 280A, from *Macroptilium atropurpureum* and *A hypogea* respectively) were used to inoculate the plants at sowing in fields which were deficient in nitrogen. Much variation was found between the landraces for the attributes measured at maturity, such as nodule number, nodule mass, shoot dry weight, shoot nitrogen and pod yield. While there was no significant change in the number and weight of nodules, overall there was a significant increase in nitrogenase activity and nitrogen content of the inoculated plants which also varied between landraces. On the contrary, non-inoculated plants were free of nodules. The amount of nitrogen fixed accounted for 80% of the total nitrogen content in the plants, which is in agreement with other similar studies (Kumaga *et al.,* 1994; Dakora *et al.,* 1992). It was also found that nitrogenase activity in most of the landraces increased significantly between 68 and 105 DAS, which represents the pod filling stage, which suggests that the crop is able to provide nitrogen during pod and seed formation. This is comparable with the conclusions of Kumaga *et al.,* (1994) who found that during reproductive development of Bambara groundnut nitrogen fixation was the primary source of nitrogen. In that same study, one of the landraces investigated fixed almost twice the amount of nitrogen as the other, highlighting the range of nitrogen fixing capacities between landraces. By quantifying such differences it will be possible to identify those landraces which can be used in breeding programmes to develop varieties with higher rates of nitrogen fixation.

In the light of Bambara groundnut's role in intercropping systems, investigating the interactions between the crops is essential. Intercropping provides great benefits in low-input agriculture on low fertility soils, as not only can it increase yields it can also ensure yield stability. The benefits of intercropping systems have thus been demonstrated in many legumes such as soybean (*Glycine max*) (Odhiambo *et al.,* 2011) and groundnut (Langat *et al.,* 2006). In order for intercropping to be of benefit, both crops need to be complimentary in the ecological niches they occupy in such a way that they do not compete for the same resources (e.g. water, nutrients and light) and consequently reduce yield. While uncommon in intensive farming involving monocultures, the method of intercropping is still important for yield stability in low-input systems, especially in Africa (Khan, 2014). Studies involving intercropping Bambara groundnut with other crops have demonstrated that for some species, intercropping increases overall yield. In some cases, incorporating Bambara groundnut into a rotation system has been identified as an efficient means of ensuring soil fertility. Work by Mukurumbira (1985) found that Bambara groundnut had a greater residual nitrogen effect than maize and groundnut, and that where rain is not a limiting factor; no nitrogen input is required for maize if it is grown after Bambara groundnut in a rotation. This is in agreement with recent work by Svubure *et al*., (2010), who assessed the soil fertility effects of different legumes when incorporated into a maize cropping system. Of all the legumes that preceded maize, growing Bambara groundnut lead to the greatest increase in maize yields (5.18 t ha $^{-1}$)

compared to soybean (4.79 t ha $^{-1}$), groundnut (4.37tha^{-1}) and Natal Sugar bean (2.89 t ha $^{-1}$). In terms of intercropping Bambara groundnut with cereals, studies have generally shown that intercrops are more successful with pearl millet than with maize and sorghum and does better when the crop is quite scattered (fewer plants) (Heller and Mushonga, 1997). Karikari (2001) grew Bambara groundnut and sorghum in rows of different combinations of intercrops and as sole crops and determined the productivity of each in terms of a Crop Performance Ratio (CPR). This value is defined as the productivity of the intercrop per unit area of ground compared with the rows consisting of a single crop. The results demonstrated that the two crops are compatible and effective in an intercropping system, and that higher yields were achieved when the Bambara groundnut population in relation to sorghum was high (>50%) than when it was low (<50%).

Karikari (2002) furthered this work by intercropping three landraces, Diphiri Cream (DipC), OMotswasele (OM6) and National Tested Seed Red (NTSR) with sorghum. The sorghum variety Segaolane was used and, as in the previous study, was grown in different ratios with Bambara groundnut (3:1, 2:2 and 1:3). Using the relative crowing coefficient (K) and relative yield total (RYT) to quantify the crop interactions, it was found that neither of the Bambara groundnut landraces inhibited or reduced the yield of sorghum. However, variation between the landraces was observed, with DipC having higher K and RYT values than the other two landraces. This suggests that DipC competes less with sorghum for resources and therefore is a more suitable landrace to use in an intercrop. As the study took place in Botswana, DipC may be a suitable target towards the development of an ideotype that can be used in intercrops with sorghum in that region. An additional benefit of intercropping Bambara groundnut is the protection it can offer as a 'trap' crop. Gworgwor (2002) conducted two trials in which Bambara groundnut and groundnut were grown separately as intercrops with varieties of sorghum that were either susceptible or resistant to *Striga hemonthica* (Del.); a parasitic plant. Groundnut and Bambara groundnut both significantly reduced the number of Striga on sorghum, with as much as a 50% reduction with groundnut and 56%-91% reduction in Striga shoot counts.

The effect of intercropped millet and Bambara groundnut was studied by Hulugalle (2009) in the Sudan savannah in Burkina Faso. The treatments were grown on both flat land and on ridges and include a millet monocrop, a millet-Bambara groundnut intercrop and a Bambara groundnut monocrop. In the intercrop treatment, light interception and root growth was not significant affected and were lower in the Bambara groundnut monocrop. Soil water content was greater for millet in the intercrop treatment on the ridges and its Relative leaf water content (RLWC) was unaltered, although it was reduced in Bambara groundnut in particular on the flat plots. Further, dry matter yield of Bambara groundnut was increased when intercropped on the tied ridging plot. These findings therefore show that yield increase and the success of a millet-Bambara groundnut intercrop lie with planting being done on ridges.

Considering both sorghum and millet are staple crops in many climate vulnerable regions of Africa, such as the Sudanese and Sahelian savannahs of West Africa (Sultan *et al.,* 2013), there is clearly great potential and a need for greater attention given to these cereal-legume intercrops.

A similar story can be seen with rice. Andika *et al.,* (2010) who investigated the performance of an intercrop involving the new rice for Africa (NERICA) rice and Bambara groundnut paying particular attention to the spatial distribution of roots in the soil. Exploring the interaction below-ground is important as the soil contains the major source of resources for crop growth. It was not until 38 days after sowing (DAS) when changes in Bambara groundnut were first observed and it was not until 52 DAS when significant increases in root length were identified. For NERICA rice, no significant changes in root diameter or length were seen at 24 DAS and 38 DAS, but by 52 DAS there were significant differences in the root diameters and in root length between the landraces. However root length was significantly higher in Bambara groundnut as the root length of rice was actually higher as a sole crop. Conversely, the volume occupied by Bambara groundnut in the soil was higher in the intercrop treatment than as a sole crop. Root densities of both crops increased after 52 DAS in the intercrop although Bambara groundnut roots were still longer. As for dry matter allocation, NERICA rice had greater allocation to the shoots when intercropped, while Bambara groundnut allocated more to the roots. This is in agreement with previous work which found that wheat (*Triticum aestivum*) increased in total above-ground biomass when intercropped with white clover (*Trifolium repens*) (Thorsted *et al.,* 2006). It was therefore apparent that rice shifted its dry matter allocation depending on whether it was grown as an intercrop or sole crop which itself is an indication of crop competition. Such competition may be beneficial, because as root length and diameter of Bambara groundnut increases, it is able to mobilise nutrients and water from a deeper layers in the soil profile. This is particularly important in times of drought where water is limited. In addition, the nitrogen fixing capacities of Bambara groundnut may lead to less competition for nitrogen when roots are intermingled. This may explain the greater dry matter allocation to the shoots of rice when intercropped. With rice being one of the most important staple crops in many African countries (IFPRI, 2012), these findings suggest great potential for an intercropping system between the two species which has not yet been fully exploited.

2.9 Concluding Comments

Meeting the needs of a changing climate and responding to the threats it will bring is without a doubt one of the most urgent issues facing Africa today. These challenges will be further magnified by a rising population, which is expected to reach 2 billion by 2050 (UNDESA, 2011). Indeed, Africa has the highest population growth rates in the world, with a tripling of the population from 230 million to 811 million in the second half of the twentieth century (FAO, 2011). With this vast population and an abundance of untapped agriculture land, a more productive Africa would not only improve food security throughout the continent, but would be able to help contribute to the rising demands of food globally.

Sustainable increases in food production and nutritional security are at the heart of ensuring food security and improving livelihoods of families and communities. What is needed however is a new approach to food production that maximises resources, is concordant with the reality and needs of subsistence farmers and is environmentally sustainable. In the context of a drier and hotter Africa, achieving sustainable yields can be helped through utilisation of crop species native to the continent of Africa that can withstand such hostile conditions. Bambara groundnut, a crop native to the semi-arid tropics of Africa, has proved to meet the characteristics required of a potential food security crop. Research has demonstrated Bambara groundnut's considerable resilience as a drought tolerant crop relative to other legumes, its ability to produce yields on marginal lands and its rich nutritional content. Further, work has shown that as an intercrop it can not only contribute to soil nitrogen content but can help boost the yields of some of the continent's most important cereal crops, such as rice, maize, millet and sorghum. Further consideration and efforts from governments, policy makers, organisations and research institutions is essential for unlocking the potential of Bambara groundnut. While the time frame is small and the task formidable, increased utilisation of Bambara groundnut and other crops indigenous to the continent of Africa, can and should play a central role in adapting to the demands of changing African climates and in ensuring the food security and livelihoods of its people.

References

Al Shareef I, Sparkes D, Azam-Ali S (2013). Temperature and Drought Stress Effects on Growth and Development of Bambara Groundnut (*Vigna subterannea* L.) *Experimental Agriculture* 50: 72-89.

Amadou HI, Bebeli PJ, Kaltsikes PJ (2001). Genetic diversity in Bambara groundnut (*Vigna subterranea L.*) germplasm revealed by RAPD markers. *Genome* 44:995-999.

Amarteifio JO, Moholo D (1998). The Chemical Composition of Four Legumes Consumed in Botswana. *Journal of Food Composition and Analysis* 11:329-332. Doi: 10.1006/jfca.1998.0595

Azam-Ali SN, Sesay A, Karikari SK, Massawe FJ, Aguilar-Manjarrez J, Bannayan M, Hampson KJ (2001). Assessing the Potential of An Underutilized Crop – A Case Study Using Bambara Groundnut. *Experimental Agriculture* 37:433-472.

Babiker AMA (1989). Growth, dry matter and yield of bambara groundnut (*Vigna subterranea*) and groundnut (*Arachis hypogaea*) under irrigated and droughted conditions. MSc thesis, University of Nottingham, UK.

Bamshaiye OM, Adegbola JA, Bamishaiye EI (2011). Bambara groundnut: an Under-Utilized Nut in Africa. *Advances in Agricultural Biotechnology* 1:60-72.

Bates BC, Kundzewicz ZW, Wu S, Palutik JP (2008). Climate Change and Water: Technical Paper of the Intergovernmental Panel on Climate Change, IPCC Secretariat, Geneva, 210 pp.

Battisti DS, Naylor RL (2009). Historical Warnings of Future Food Insecurity with unprecedented Seasonal Heat. *Science* 9:240-244.

Berchie JN, Opoku M, Adu-Dapaah H, Agyemang A, Sarkodie-Addo J, Asare E, Addo J, 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* 7(2): 250-256.

Berchie JN, Adu-Dapaah HK, Dankyi AA, Plahar WA, Nelson-Quartey F (2010). Practices and Constraints in Bambara Groundnuts Production, Marketing and Consumption in the Brong Ahafo and Upper-East Regions of Ghana. *Journal of Agronomy* 9(3): 111-118.

Berg A, de Noblet-Ducoudré N, Sultan B, Lengaigne M, Guimberteau M (2013). Projections of climate change impacts on potential C4 crop productivity over tropical regions. *Agricultural and Forestry Meteorology* 170:89-102.

Boko M, Niang I, Nyong A, Vogel C (2007) Africa. In: Parry M et al (eds) Climate Change Adaptation and Vulnerability: Contribution of Working Group II to the IV Assessment Report of the IPCC Panel on Climate Change. Cambridge University Press, Cambridge and New York, pp 433–467.

Botero C, Weissing FJ, Wright JW, Rubenstein DR (2015). Evolutionary tipping points in the capacity to adapt to environmental change. *PNAS* 112: 184-189.

CABI (2009). Rainfed Agriculture: Unlocking the Potential. Cab International.

Calzadilla A, Zhu T, Redhanz K ,Tol RSJ, Ringler C (2009). Economy wide Impacts of Climate Change in Sub-Saharan Africa, IFPRI Discussion Paper No. 873 (Washington, DC: International Food Policy Research Institute).

Connolly-Boutin L, Smit B (2015). Climate change, food security, and livelihoods in sub-Saharan Africa. *Reg Environ Change* Advance Online Publication. DOI: 10.1007/s10113-015-0761-x

Collinson ST, Azam-Ali SN, Chavula KM, Hodson DA (1996). Growth, development and yield of bambara groundnut (*Vigna subterranea*) in response to soil moisture. *Journal of Agricultural Science* 126:307-318.

Dakora F (1998). Nodule Function in Symbiotic Bambara Groundnut (Vigna subterranea L.) and Kersting's Bean (Macrotyloma geocarpum L.) is Tolerant of Nitrate in the Root Medium. *Annals of Botany* 82:687-690.

Devereux S (2009). The Malawi Famine of 2002. *Institute of Development Studies* 33:70-78.

Diao X, Hazell P, Thurlow J (2010). The Role of Agriculture in African Development. *World Development* 38:1375-1383.

Druyan L M (2011). Studies of 21st-century precipitation trends over West Africa *Int. J. Climatol.* 31:1415–572.

Doku EV, Karikari SK (1971). Bambara Groundnut. *Economic Botany* 25:255-&.

Easterling W, Aggarwal P, Batima P, Brander K, Erda L, Howden M, Kirilenko A, Morton J, Soussana JF, Schmidhuber J, Francesco, Tubiello F (2007). Food, Fibre and Forest Products. In *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change,* ed. Martin L. Parry, Osvaldo F. Canziani, Jean P. Palutikof, Paul J. van der Linden, and Clair E. Hanson. Cambridge, UK: Cambridge University Press.

Ebert AW (2014). Potential of Underutilized Traditional Vegetables and Legume Crops to Contribute to Food and Nutritional Security, Income and More Sustainable Production Systems. *Sustainability* 6:319-335.

FAO (2014). The Sahel Crisis. (Available at www.fao.org).

FAO (2013). Climate-Smart Agriculture Sourcebook. (Available at http://www.fao.org/climatechange/climatesmart/en/)

FAO (2013). INFOODS List of underutilized species contributing to the Nutritional Indicators for Biodiversity Version 1.2 (December 2013) (available at: http://www.fao.org/infoods/infoods/food-biodiversity/en/).

FAO (2012). News Article: Neglected crops need a rethink (available at www.fao.org/news/story/en/item/166368/icode/).

FAO. 2011 The status of food insecurity in the world. Rome, Italy: Food and Agriculture Organization.

FAO (2010). FAOSTAT, 2010 data (Available at www.faostat.fao.org).

FAO (2008a). Climate change adaptation and mitigation in the food and agriculture sector. High-level conference on food security – the challenges of climate change and bioenergy. (available at ftp://ftp.fao.org/docrep/fao/ meeting/013/ai782e.pdf).

FAO (2005). FAO and the challenge of the Millennium Development Goals. Discussion Paper for the Special Event on "Impact of conflicts and governance on food security, and FAO's role and adaptation for achieving the MDGs", on the occasion of the 31st session of the Committee on World Food Security, May 2005, at FAO headquarters

FAO (2005). FAO Newsroom: Malawi facing serious food crisis. (Available at www.fao.org/newsroom

Ferguson BJ, Indrasumunar A, Hayashi S, Lin M-H, Lin Y-H, Reid DE, Gresshoff PM (2010) Molecular analysis of legume nodule development and autoregulation. *J Integr Plant Biol* 52:61–76

Fischer, Günther, Mahendra Shah, Francesco N. Tubiello, Harrij van Velthuizen (2005). Socio-economic and Climate Change Impacts on Agriculture: An Integrated Assessment, 1990-2080. *Philosophical Transactions of the Royal Society B*: *Biological Sciences* 360: 2067–83.

Ford JD, Berrang-Ford L, Bunce A, McKay C, Irwin M, Pearce T (2014). The status of climate change adaptation in Africa and Asia. *Reg Environ Change* DOI 10.1007/s10113-014-0648-2.

Frankea E (2014). Africa and the Green Revolution A Historical Perspective. *Wageningen Journal of Life Science* 70: 17-24. doi:10.1016/j.njas.2014.01.003

Gitz, V. & Meybeck, A. 2012. *Risks, vulnerabilities and resilience in a context of climate change*. In FAO & OECD Building Resilience for Adaptation to Climate Change in the Agriculture Sector. Rome.

Gowda CLL, Upadhyaya HD, Ghaffar MA (2007). *Importance of under-utilized indigenous legumes in Asia-pacific region. Acta Horticulturae 752:95-98.*

Graham PH, Vance CP (2003). Legumes: Importance and Constraints to Greater Use. Plant Physiology 131:872-877.

Hagemann S, Chen C, Clark DB, Folwell S, Gosling SN, Haddeland I, Hanasaki N, Heinke J, Ludwig F, Voss F, Wiltshire AJ (2013). Climate change impact on available water resources obtained using multiple global climate and hydrology models. *Earth Syst. Dynam* 4:129-144.

Hampson KJ, Azam-Ali SH, Sesay A, Mukwaya S and Azam-Ali SN (2001). Assessing opportunities for increased utilisation of bambara groundnut in Southern Africa. In preparation for submission to Journal of Science, Food and Agriculture.

Heller J, Begemann F, Mushonga J (1997). Bambara groundnut (*Vigna subterranea* (L.) Verdc.). Promoting the conservation and use of underutilized and neglected crops. 9. Proceedings of the workshop on Conservation and Improvement of Bambara Groundnut (*Vigna subterranea* (L.) Verdc.), 14–16 November 1995, Harare, Zimbabwe. Institute of Plant Genetics and Crop Plant Research, Gatersleben/Department of Research & Specialist Services, Harare/International Plant Genetic Resources Institute, Rome, Italy.

Hepper FN (1963). The Bambara groundnut (*Voandzeia subterranea*) and Kersting's groundnut (*Kerstingiella geocarpa*) wild in west Africa. *Kew Bull* 16:395–407.

Holden C (2009). Climate Change. Higher Temperatures Seen Reducing Global Harvests. *Science* 323:193.

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (2001). Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Human influences will continue to change atmospheric composition throughout the 21st century. Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York

Hulme M, Doherty R, Ngara T, New M, Lister D (2001). African climate change: 1900-2100. *Climate Research* 17:145-168.

International Food Policy Research Institute (IFPRI) (2008). Agricultural Growth and Investment Options for Poverty Reduction in Malawi. (Available at www.ifpri.org).

International Food Policy Research Institute (IFPRI) (2012). Southern African Agriculture and Climate Change: A comprehensive analysis – Kenya. (Available at www.ifpri.org).

International Food Policy Research Institute (IFPRI) (2012). Southern African Agriculture and Climate Change: A comprehensive analysis – Zimbabwe. (Available at www.ifpri.org).

International Food Policy Research Institute (IFPRI) (2012). Food and agriculture in Ethiopia. University of Pennsylvania Press. Philadelphia

International Food Policy Research Institute (IFPRI) (2011). Climate Change Impacts on Food Security in Sub-Saharan Africa: Insights from Comprehensive Climate Change Modeling. (Available at www.ifpri.org).

International Union for Conservation of Nature (IUCN) (2011). Wani Case Studies: Pangani River Basin, Tanzania. (Available at www.iucn.org)

International Monetary Fund (2012). Regional Economic Outlook: Sub-Saharan Africa, Maintaining Growth in an Uncertain World. World Economic and Financial Surveys (Available at: https://www.imf.org)

Intergovernmental Panel on Climate Change (IPCC) (2013). Fifth Assessment Report (AR5). Cambridge University Press: Cambridge, United Kingdom and New York

Intergovernmental Panel on Climate Change (IPCC) (2007). IPCC Fourth Assessment Report (AR4). Cambridge University Press: Cambridge, United Kingdom and New York

James R, Washington R (2013). Changes in African temperature and precipitation associated with degrees of global warming. *Climatic Change*. 117(4): 859-872.

Jensen ES, Peoples MS, Boddey RM, Gresshoff, Hauggaard-Nielsen H, JR B, Morrison MJ (2011). Legumes for mitigation of climate change and the provision of feedstock for biofuels and biorefineries. A review. *Agronomy for Sustainable Development* 32:329-364.

Jerven M, Duncan ME (2012). Revising GDP estimates in Sub-Saharan Africa: Lessons from Ghana. *African statistical Journal* 15:12-24

Jørgensen ST, Liu F, Ouedraogo, Ntundu WH, Sarrazin J, Christiansen JL (2010). Drought Responses of Two Bambara Groundnut (Vigna subterranea L. Verdc.) Landraces Collected from a Dry and a Humid Area of Africa. *Journal of Agronomic and Crop Science* 196: 412-422.

Karunaratne AS (2009). Modelling the response of bambara groundnut (Vigna sub-terranea L. Verdc.) for abiotic stress. In: PhD Thesis, School of Biosciences. University of Nottingham, UK, 176pp.

Karunaratne AS, Azam-Ali SN, Al-Shareef I, Sesay A, Jørgensen ST, Crout NMJ (2010). Modelling the canopy development of bambara groundnut. Agric. *ForestMeteorol* 150: 1007–1015.

Khan ZR, Midega CAO, Pittchar JO, Murage AW, Birkett MA, Bruce TJA, Pickett JA (2014). Achieving food security for one million sub-Saharan African poor through push – pull innovation by 2020. *Philos Trans R Soc Lond B Biol Sci.* 369: 20120284.

Khan ZR, Midega CAO, Hassanali A, Pickett JA, Wadhams LJ (2007). Assessment of different legumes for the control of *Striga hermonthica* in maize and sorghum. *Crop Sci*. 47: 728–734.

Knox J, Hess T, Daccache A, Wheeler T (2012). Climate change impacts on crop productivity in Africa and South Asia. *Environmental Research Letters* 7: 034032.

Kruger AC, Shongwe S (2004). Temperature trends in South Africa: 1960-2003. *International Journal of* Climatology. 24(15): 1929-1945.

Lal R, Delgado JA, Groffman PM, Millar N, Dell C, Rotz A (2011). Management to mitigate and adapt to climate change. *Soil and Water Conservation* 4:276-285.

Linnemann AR, Azam-Ali SN (1993). Bambara groundnut (Vigna subterranea). In Underutilized Crops: Pulses and Vegetables, 13±57 (Ed. J. T. Williams). London: Chapman & Hall.

Linnemann AR (1990). Cultivation of bambara groundnut in Western Province, Zambia. Report of a Field Study. Trop. Crops Comm. No. 16, Wageningen Agricultural University.

Liu J, Folberth C, Yang H, Rockström J, Abbaspour K, Zehnder AJB (2013). A Global and Spatially Explicit Assessment of Climate Change Impacts on Crop Production and Consumptive Water Use. *PLoS ONE*. 8: e57750.

Lobell DB, Gourdji SM (2012). The Influence of Climate Change on Global Crop Productivity. *Plant Physiology.* 160 (4): 1686-1697.

Lobell DB, Marshall B, Tebaldi C, Mastrandrea MD, Falcon WP, Naylor RL (2008). Prioritizing Climate

Change Adaptation Needs for Food Security in 2030. *Science* 319 (5863): 607–10.

Lobell DB, Field CB *(*2007). Global scale climate-crop yield relationships and the impacts of recent warming. *Environmental Research Letters* 2:7.

Lyon B, DeWitt DG (2012). A recent and abrupt decline in the East African long rains. *Geophysical Research Letters* 39(2).

Lynd LR, Woods J (2011). Perspective: A new hope for Africa. *Nature* 474: S20–S21.

Mabhaudi T, Chibaradaba T, Chimonyo V, Modi A (2018). Modelling climate change impact: A case of bambara groundnut (*Vigna subterranea*). *Physics and Chemistry of the Earth* 105: 25-31.

Mabhaudi T, Chibarabada T, 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.

Massawe FJ, Mwale SS, Azam-Ali SN, Roberts JA (2005). Breeding in bambara groundnut (*Vigna subterranea* (L.) Verdc.): strategic considerations. *African Journal of Biotechnology* 4:463-471.

Massawe FJ, Dickinson JA, Roberts JA, Azam-Ali SN (2002). Genetic diversity in bambara groundnut (*Vigna subterranea* (L). Verdc) landraces revealed by AFLP markers. *Genome* 45:1175-1180.

Mayes S, Massawe FJ , Alderson PG, Roberts JA, Azam-Ali SN, Hermann M (2011). The potential for underutilized crops to improve security of food production. *Journal of Experimental Biology* 63: 1075-1079.

Mwale SS, Azam-Ali SN, Massawe FJ (2007) Growth and development of bambara groundnut (Vigna subterranea) in response to soil moisture – 1. Dry matter and yield. *Euro. J. Agron* 26:345–353.

Mazahib, AM, Nuha, MO, Salawa IS, Babiker EE (2013) Some nutritional attributes of bambara groundnut as influenced by domestic processing. *International Food Research Journal* 20*:* 1165-1171

Mkandawire, CH (2007). Review of bambara groundnut (*Vigna subterranea* (L.) Verdc.) production in Sub-Sahara Africa. *Agric. J*. 2: 464-470.

Mohino E, Janicot S, Bader J (2011). Sahel rainfall and decadal to multi-decadal sea surface temperature variability. *Climate Dynamics*. 37(3): 419-440.

Mukakalisa C, Kandawa-Schulz M, Mapaure I (2013). Genetic diversity in landraces of Bambara groundnut found in Namibia using RAPD markers. *Acta Horticulturae* 979:683-688.

Müller C (2013). African lessons on climate change risks for agriculture. *Ann. Rev. Nutr*. 33: 395-411.

Mwale SS, Azam-Ali SN, Massawe FJ (2007) Growth and development of bambara groundnut (Vigna subterranea) in response to soil moisture – 1. Dry matter and yield. *Euro. J. Agron* 26:345–353.

Mwale SS, Azam-Ali SN, Massawe FJ (2007). Growth and development of bambara groundnut (Vigna subterranea) in response to soil moisture. 2. Resource capture and conversion. *European Journal of Agronomy* 26:354-362.

Najafi MBH, Lee BH (2014). Biotechnology and its impact on food security and safety. *Current Nutrition and Food Science* 10:94-99.

Nikulin, G, Jones C, Giorgi F, Asrar G, Büchner M, Cerezo-Mota R, Christensen OB, Déqué M, Fernandez J, HänslerA , van Meijgaard E, Samuelsson P, Sylla MP, Sushama L (2012). Precipitation climatology in an ensemble of CORDEX-Africa regional climate simulations. *Journal of Climate*. 25(18): 6057-6078.

Qaim M (2011). Genetically modified crops and global food security. *Frontiers of Economics and Globalization* 10:29-54.

Ringler C, Zhu T, Cai X, Koo J, 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).

Rost S, Gerten D, Hoff H, Lucht W, Falkenmark M, Rockström J (2009). Global potential to increase crop production through water management in rainfed agriculture. *Environ.Res.Lett* 4 (9pp).

Romney DL, Thorne P, Lukuyu B, Thornton PK (2003). Maize as food and feed in intensive smallholder systems: management options for improved integration in mixed farming systems of east and southern Africa. *Field Crops Res*. 84: 159–168. (doi:10.1016/S0378-4290(03)00147-3)

Ruiz KB, Biondi S, Oses R, Acuña-Rodríguez IS, Antognoni F, Martinez-Mosqueira EA, Coulibaly A, Canahua-Murillo A, Pinto M, Zurita-Silva A, Bazile D, Jacobsen SE, Molina-Montenegro MA (2014). Quinoa biodiversity and sustainability for food security under climate change. A review. *Agronomy for Sustainable Development* 34:349-359.

Sambo BE (2014). Endangered, Neglected, Indigenous Resilient Crops: A Potential against Climate Change Impact for Sustainable Crop Productivity and Food Security. *IOSR Journal of Agriculture and Veterinary Science* 7:34-41.

Schaffnit-Chatterjee (2014). Agricultural value chains in Sub-Saharan Africa. From a development challenge to a business opportunity. *Deutsche Bank Research.*

Scherr SJ, Buck LE, Majanen T, Milder JC, Shames S (2011). Scaling-up landscape investment approaches in Africa: where do private market incentives converge with landscape restoration goals? Background paper for the Investment Forum on Mobilizing Investment in Trees and

Landscape Restoration. Washington D.C., EcoAgriculture Partners and Program on Forests (PROFOR).

Schlenker W and Lobell D (2010). Robust negative impacts of climate change on African agriculture. *Environmental Research Letters* 5 (1): 014010.

Shongwe ME, van Oldenborgh FJ, van den Hurk B, van Aalst M (2011). Projected changes in mean and
extreme precipitation in Africa under global warming. Part II: East Africa. *Journal of Climate* 24:3718-3733.

Singh RP, Hodson DP, Huerta-Espino J, Jin Y, Bhavani S, Njau P, Herrera-Foessel S, Singh PK, Singh P, Govindan V (2011). The emergence of Ug99 races of the stem rust fungus is a threat to world wheat production. *Annual Review of Phytopathology* 49:465-481.

Smith D, Vivekananda J (2007). A Climate of Conflict: The Links Between Climate Change, Peace and War. *International Alert.* London.

Siise A, Massawe FJ (2013). Microsatellites based marker molecular analysis of Ghanaian bambara groundnut (Vigna subterranea (L.) Verdc.) landraces alongside morphological characterization. *Genetic Resources and Crop Evolution* 60:777-787.

Somta P, Chankaew S, Rungnoi O, Srinives P, Scoles G (2011). Genetic diversity of the Bambara groundnut (Vigna subterranea (L.) Verdc.) as assessed by SSR markers. 54:898-910,

Sprent JI, Odee DW, Dakora FD (2009). African legumes: a vital but under-utilized resource. *Journal of Experimental Botany* 61:1257-1265.

Sultan B, Roudier P, Quirion P, Alhassane A, Muller B, Dingkuhn M, Ciais P, Guimberteau M, Traore S, Baron C (2013). Assessing climate change impacts on sorghum and millet yields in the Sudanian and Sahelian savannas of West Africa. *Environmental Research Letters* 8:014040.

Tilahun H, Teklu E, Michael M, Fitsum H, Awulachew SB (2011). Comparative performances of irrigated and rainfed agriculture in Ethiopia. *World Applied Sciences Journal* 14:235-244.

UNDESA (United Nations Department of Economic and Social Affairs) (2011). World Population Prospects: The 2010 Revision. New York: United Nations Department of Economic and Social Affairs, Population Division. www.un.org/esa/population/.

United Nations Office for the Coordination of Humanitarian Affairs (OCHA (2014). Strategic Response Plan: Sahel Region (available at www.unocha.org).

United Nations Office for the Coordination of Humanitarian Affairs (OCHA) (2011). Eastern Africa Drought Humanitarian Report. (Available at www.reliefweb.int).

United Nations Development Programme (UNDP) (2012). Africa Human Development Report 2012. Regional Bureau for Africa (RBA). (Available at www.undp.org/africa).

United Nations Development Programme (UNDP) (2006). (Available at www.undp.org).

Várallyay G (2010). The impact of climate change on soils and on their water management. *Agronomy Research* 8:385-396.

Vurayai R, Emongor V, Moseki B (2011). Physiological Responses of Bambara Groundnut (*vigna subetteranea* L. Verdc) to Short Periods of Water Stress During Different Developmental Stages. *Asian J. Agric. Sci.* 3:37-43.

Waha K, Müller C, Rolinski C (2013). Separate and combined effects of temperature and precipitation change on maize yields in sub-Saharan Africa for mid- to late-21st century. *Global Planet. Change* 106:1-12.

Williams AP, Funk C, Michaelsen J, Rauscher SA, Robertson I, Wils THG, Koprowski M, Eshetu Z, Loader NJ (2012). Recent summer precipitation trends in the Greater Horn of Africa and the emerging role of Indian Ocean sea surface temperature. *Climate Dynamics* 39:2307-2328.

3 Above and below-ground physiological traits associated with Bambara groundnut (*Vigna subterranea* (L.) Verdc) adaptation in irrigated and drought conditions

3.1 Introduction

Currently regarded as an underutilised crop, Bambara groundnut is grown mainly in sub Saharan African countries such as Zimbabwe, South African and Kenya, where its seeds can be eaten fresh, as a pulse or can be used to make flour. Known in Madagascar as 'a seed that satisfies', it has a high protein and carbohydrate content (Azam-Ali *et al*, 2001). As a legume it adds nitrogen to the soil via nitrogen fixation, meaning it can be a valuable crop in rotations where it can contribute to soil fertility. At present a true variety of the crop does not exist and the germplasm exists in the form landraces which have been preserved by farmers. In those regions where Bambara groundnut is grown, water availability is one the major limiting factors to yield.

Research suggests certain physiological and metabolic traits contribute to the plant's resilience, namely a reduction of transpiration by stomatal control, a high root: shoot biomass ratio, maintenance of leaf turgor, an increase in partitioning of dry matter to roots and a reduction in leaf area development (Collinson, 1996; Collinson *et al*., 1997).

Mwale et al*.,* (2007) observed that landraces responded to drought through reductions in canopy size and leaf area expansion, as well as total dry matter and pod dry matter. Differences in rates of growth amongst landraces were identified which play an important role in drought tolerance. For example, the S19-3 landrace, which is from an environment characterised by low rainfall and a short growing season, performed better under drought conditions than Dip C and Unisa-red which are from regions of higher rainfall and a longer growing season. The greater yields shown in S19-3 were attributed to its faster rate of growth and development, with yield formation occurring much sooner than the other landraces and has been shown in other studies (Karunaratne *et al*., 2010). These differences demonstrate the range of characteristics that exist among landraces that can be of use in crop management and for the selection of traits in breeding programmes. Such findings highlight the need to better understand the underlying mechanisms and traits can confer these differences. Further, yields found this study (1.65 t ha^{-1}) were on average higher than what has been reported from cowpea (0.3-0.5 t ha^{-1}) under similar conditions (Leport *et al.,* 1999), further underscoring the value of this crop.

In environments where water is a major limiting factor, roots have a direct and essential role in the maintenance of water supply. This is done through both the quantity of roots and the depth of rooting into the soil (Sinclair and Weiss, 2010). When water is stored throughout the soil profile and becomes scarce, the depth to which roots and reach becomes a major factor in maintaining water supply for crops. It is common for crops to fill their grain during times of infrequent rain and when stored moisture is utilised (Gregory, 2006); something that will become more problematic throughout the semi-arid regions of Africa with regional precipitation changes.

As well as having a compact, well developed taproot, it has been shown that in response to water stress Bambara groundnut adjusts both its root and shoot biomass (Giller, 2001). In one of the first studies investigating drought, Collinson *et al*., (1999) observed that plants grown in the drought treatments exhibited increased root growth and were found deeper in the soil profile than those in the irrigated treatment. Similarly, when grown in an intercrop with New Rice for Africa (NERICA) rice (*Oryza sativa*), Bambara groundnut showed the greatest increase in root length and occupied a greater volume in the soil (Andika *et al.,* 2010). Furthermore, root length was greater in Bambara groundnut when grown as intercrop than as a sole crop, suggesting Bambara groundnut may be able to adjust to conditions when resources are more limited. Deep rooting as a means of maintaining water supply is well documented in a variety of species, such as the common bean (*Phaseolus vulgaris* L.) whose roots under normal conditions have reported to reach 0.7-0.8m into the soil profile while drought tolerant lines reached at least 1.2m (Sponchiado et al 1989). Even amongst major cereal crops, genes are being identified that confer greater downward bending of roots and increase yield under drought conditions (Uga *et al*. 2013). As well as depth, root thickness and the ability to penetrate compact soil layers have been linked to drought avoidance. Lafitte *et al*., (2001) found that rice (*Oryza sativa)* cultivars with superior water capture capacity displayed thicker roots, wider vessels and a greater proportion of roots distributed below 15cm than other, less water retaining cultivars. Mwale *et al.,* (2007) confirmed the deep rooting behaviour of Bambara groundnut, as those plants in the irrigated treatment extracted water from the top 50cm of the soil, while the roots of those experiencing drought were found throughout the soil profile, some reaching as far 90cm.

Water use and growth prior to flowering has been found to be important in environments which are highly dependent on growing season rainfall in regards to barley (*Hordeum vulgare* L.) yields (Wahbi and Gregory, 1989). Further, studies of seedlings under drought conditions have identified some important characters. Again with barley, seedling grains of two barley landraces from dry environments produced more lateral roots with a faster rate of expression under drought conditions than other genotypes (Wahbi and Gregory, 1995). Similarly in seedlings of wheat (*Triticum aestivum* L.), Ma *et al.,* (2012) demonstrated that the drought tolerant cultivar Luohan 7 was able to achieve higher root water uptake than the drought sensitive cultivar by maintaining greater root biomass and enhancing root vitality. Relative to the other characters, the behaviour of roots, especially at different stages of plant growth, has so far received little attention with Bambara groundnut. In the effort to better understand Bambara groundnut's substantial capacity to withstand periods of drought and identify the most important characters for drought tolerance amongst landraces, the role of roots and their behaviour under water stress need to be investigated.

3.1.1 Objectives

The objectives of this study were to assess the impact of drought on stomatal conductance, chlorophyll content and root parameters of landraces of Bambara groundnut.

3.2 Methodology

3.2.1 Site and Materials

This trial took place at the University of Nottingham Malaysia Campus in Semenyih, Malaysia, from May to August of 2014. Plants were grown in a screen house on campus, the walls of which are made from plastic mesh allowing for ventilation and light to pass through. The soil used was a sandy loam soil, which was brought to the shade house from the Field Research Centre and had a pH of 4.2. Two landraces of Bambara groundnut were evaluated under irrigated and drought conditions: Burkina from Burkina Faso, and Nav 4 from Ghana. Both showed successful germination rates in earlier preliminary trials and in other studies the former has displayed greater drought tolerance (Berchie *et al*., 2012).

Image 1.0. PVC columns

Seeds were sown on 15^{th} May 2014 in 24 PVC columns which were 75cm in height and 20cm in diameter. Data was analysed using Genstat statistical software version 14, in order to carry out the Student's t-tests and Analysis of Covariance (ANOVA). T-tests were used largely due to the smallness of the sample size.

3.2.2 Treatment and Design

Three seeds were sown per column which were then thinned to one plant per column four days after seedling emergence.

The experiment was arranged as a randomised complete block design with two treatments (watered and drought). The treatments were completely randomised within each block. This was chosen as the treatment number was low and provided ease for statistical analysis.

The irrigated or control plants were well watered by hand to roughly 75% field capacity of the soil throughout the experiment and was maintained through use of a soil moisture probe (Theta probe ML-2x connected to an HH2 moisture meter). On the other hand the drought treatment received the same irrigation regime up until grain/pod filling at 88 DAS (11/8/2014), after which no further irrigation was applied. This stage was chosen as Bambara groundnut has been shown to be particularly susceptible to water stress related damage during pod filling (Vurayai *et al*., 2011; Jørgensen *et al*., 2011).

3.2.3 Procedure

Each column was subject to fertiliser treatments one week before sowing which included 0.61g of urea, 1.82g singe super phosphate and 0.93g muriate of potash. Plant emergence was measured on all plants starting from 6 DAS until full emergence was achieved, which was recognised as when seedlings showed 90% emergence. After full emergence, plant height, chlorophyll content and stomatal conductance were measured at various stages. Chlorophyll content was measured weekly on the abaxial surface using a SPAD-502 chlorophyll meter, with readings always taking place from 8:00am, while stomatal conductance was measured from 11:00am using a Leaf Porometer, Decagon Devices. Upon final harvest, leaf area index, final leaf number, pod number and weight and dry and fresh weights of leaves and stems were taken.

For root analysis, columns were opened and soil was washed off with water to access roots. Roots were then taken to the lab and washed to remove dirt, stones and other organic matter present in the soil. Images of roots were generated and analysed by the root imaging software WinRHIZO. Lastly, roots were weighed to obtain fresh weight and then dried at 80°C for 48 hours before being re-weighed for dry weights. Statistical analysis of the data was carried out using a single factor Analysis of Variance (ANOVA) using GenStat (16th Edition). An example of analysed root images can be seen in image 4.0.

3.3 Results

Overall, gradually decreasing soil moisture content affected various physiological characters of both landraces. Plant height and canopy spread decreased in both landraces after the onset of the drought treatment, with Burkina landraces generally being taller and with thicker canopies (see fig 4.0). Differences in canopy density and leaf colour could also be seen before treatments were imposed, with a number of Burkina plants showing a lighter shade of green than Nav 4 which had mostly dark green leaves, shown in image 2.0. This is reflected in the Chlorophyll content measurements which were significantly higher in Burkina landraces when plants were well watered ($P<0.05$), however there was no significant change in chlorophyll content in response to water stress for either landraces ($P>0.1$).

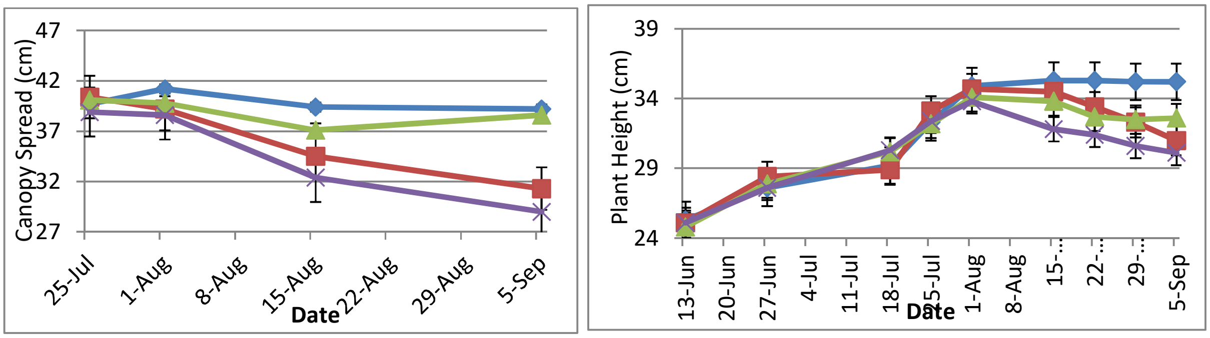


Figure 4.0: Canopy spread and plant heights of two landraces of Bambara groundnut, Burkina and Nav 4. Data points represent means values ± standard deviation, n = 6. Burkina control ( ) Burkina drought ( ), Nav 4 control ( ), Nav 4 drought ( ).

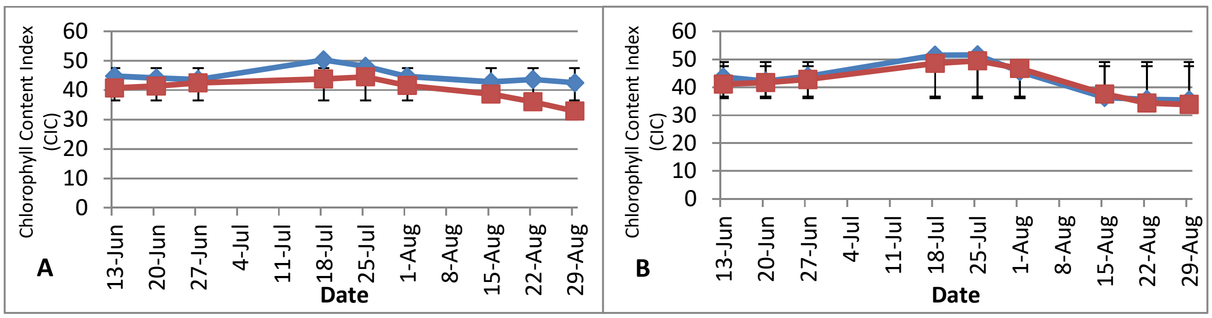


Figure 5.0: Chlorophyll Content Index (CIC) of two landraces of Bambara groundnut of control plants (A) and plants under drought treatment (B). Data points represent means values ± standard deviation, n = 6. Burkina ( ) Nav 4 ( ).

Image 2.0 Leaf colours of well-watered Nav 4 (A) and Burkina (B) landraces of Bambara groundnut.

While Burkina seedlings emerged on average one day earlier, Nav 4 showed the first signs of above-ground pod production. Pods appeared first on Nav 4 at 12 weeks after sowing whilst none could be seen in Burkina plants until appearing in one plant 7 days later (13 weeks after sowing). At 14 weeks after sowing, considerably more pods could be seen on Nav 4 landraces than Burkina in the well watered treatment (see image 3.0).

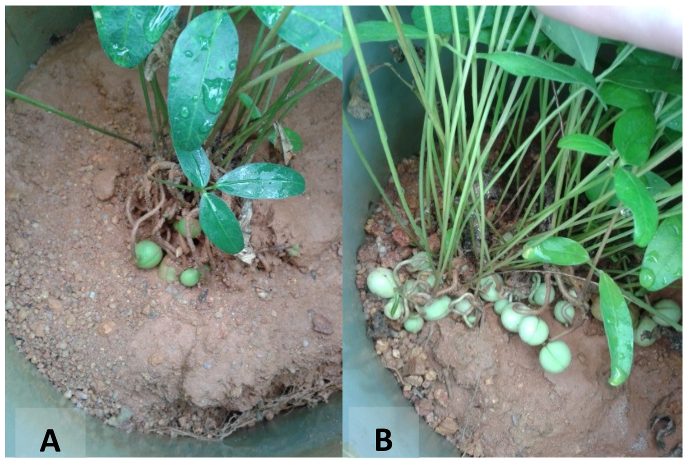


Image 3.0 Above ground pods of well-watered Burkina (A) and Nav 4 (B) landraces at 14 weeks after sowing.

Observations of stomatal activity show that Nav 4 had a generally higher rate of stomatal conductance throughout the experiment for the control treatment, however this was not significant ($P>0.1$). Yet for both landraces, stomatal conductance exhibited a significant decrease in water stressed plants for both landraces ($P>0.01$), demonstrating a physiological response to the drought conditions. Nav 4 had both the highest and lowest stomatal conductance readings during the drought treatment, at 40.3 mmol m^{-2} m^{-1} and 17.8 mmol m^{-2} m^{-1}, respectively.

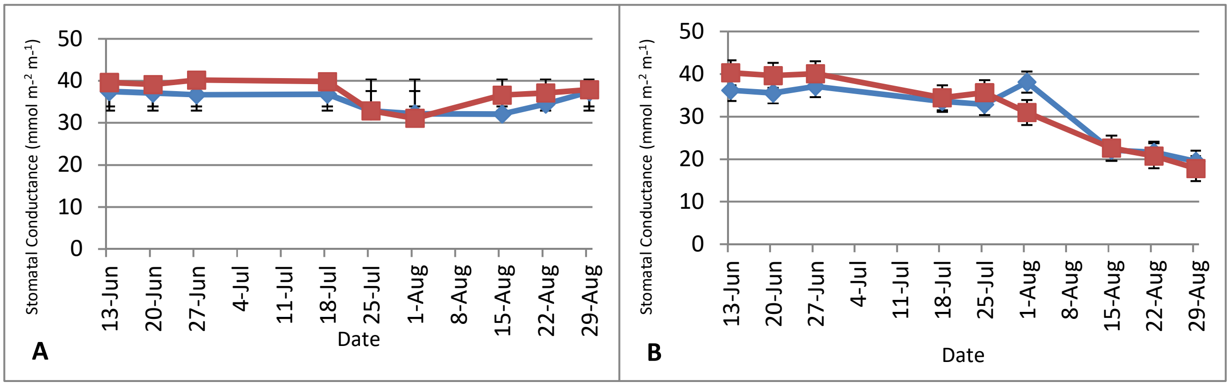


Figure 6.0 Stomatal Conductance (mmol m-^{2} m-^{1}) of two landraces of Bambara groundnut under well watered (A) and drought conditions (B). Burkina ( ) Nav 4 ( ). Data points represent means values ± standard deviation, n = 6.

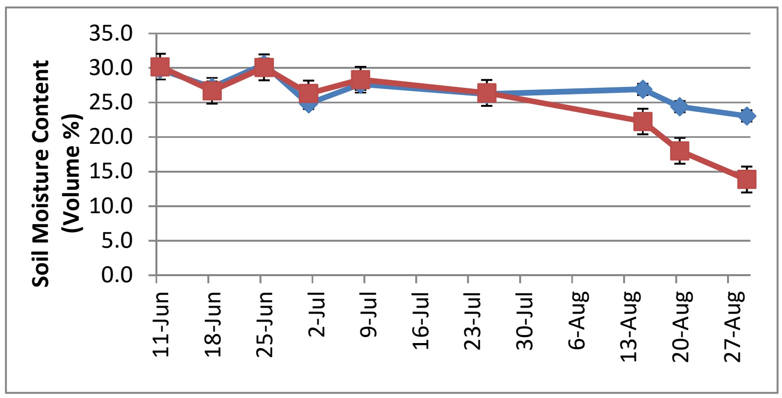


Figure 7.0 Soil moisture content (Volume %) of soils used for the control ( ) and drought ( ) treatments. Data points represent means values ± standard deviation, n = 6.

Final pod number was on average higher with Burkina in the watered treatment, although this was not significant ($p>0.5$), whereas under drought conditions Nav 4 had significantly more pods (see figure 8.0). Further, pod number was reduced in Nav 4 in drought conditions. Under watered conditions, Burkina had a higher average pod number of 23.6 compared to 16.1 in Nav 4. All Burkina plants in the watered treatment produced a minimum of 20 pods, whilst in Nav 4 some produced as low as 5 and only 2 plants produced more than 20 pods (see table 1.0). However during the drought treatment 4 out of 6 Burkina plants produced no pods whereas pods were found on all Nav 4 plants (see table 2.0).

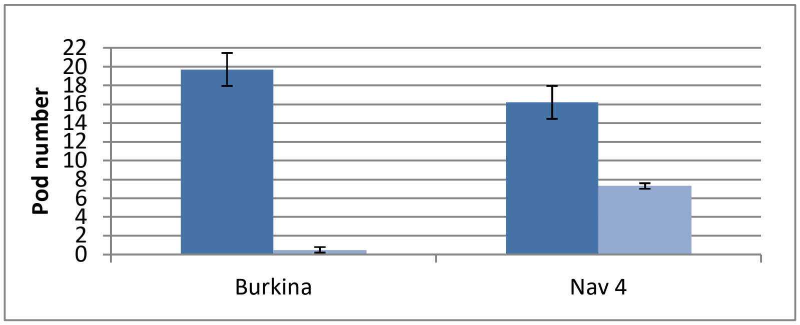


Figure 8.0. Final pod number of Burkina and Nav 4 landraces under watered (■) and drought (■) conditions. Data points represent means values ± standard deviation, n = 3.

Table 1.0 Final leaf dry weight, leaf number, pod number and weight of Burkina and Nav 4 landraces under watered conditions.

	Plant number	Leaf Dry weight	leaf number	pod number	pod weight (g)
Burkina	1	8.9	205	20	35.5
	2	10.4	215	26	21.5
	3	13.6	260	0	0
	4	8.9	250	20	25.2
	5	8.2	220	27	20.5
	6	7.1	234	25	38.1
Nav 4	1	12.7	240	5	2.3
	2	n/a	<80	5	2.1
	3	4.5	180	14	9.3
	4	5.5	171	10	8.8
	5	5.4	185	32	24.7
	6	8.3	170	31	18

Table 2.0 Final leaf dry weight, leaf number, pod number and weight of Burkina and Nav 4 landraces under drought conditions.

	Plant number	Leaf dry weight	leaf number	pod number	pod weight (g)
Burkina	1	4.2	130	0	0
	2	8	220	0	0
	3	7.4	221	2	1.9
	4	9	215	0	0
	5	8.7	141	1	0.5
	6	8.8	250	0	0
Nav 4	1	7.4	211	2	0.7
	2	4.9	154	6	3
	3	5.9	135	9	4.9
	4	8	170	1	0.3
	5	5.4	110	10	7.4
	6	4.3	115	16	6.9

3.3.1 Results of root analysis

Vertical length of roots was significantly longer in Burkina in the drought treatment ($p<0.05$) but not for the watered treatment ($p>0.1$). Further, there was no significant change in vertical root length between treatments for Burkina ($p>0.5$) or Nav 4 ($p>0.1$), however the average of the latter did decrease in the drought treatment. Root surface area was significantly greater in Burkina in the watered treatment ($p<0.05$) but not the drought treatment ($p>0.1$). The highest surface area was found with Burkina in the drought treatment with a value of 2599.27cm^2. Final root dry matter was significantly greater in Burkina for the drought treatment ($p<0.05$) but only marginally insignificantly different for the watered treatment ($p>0.05$). Raw data used for these analyses is shown in tables 3 and 4.

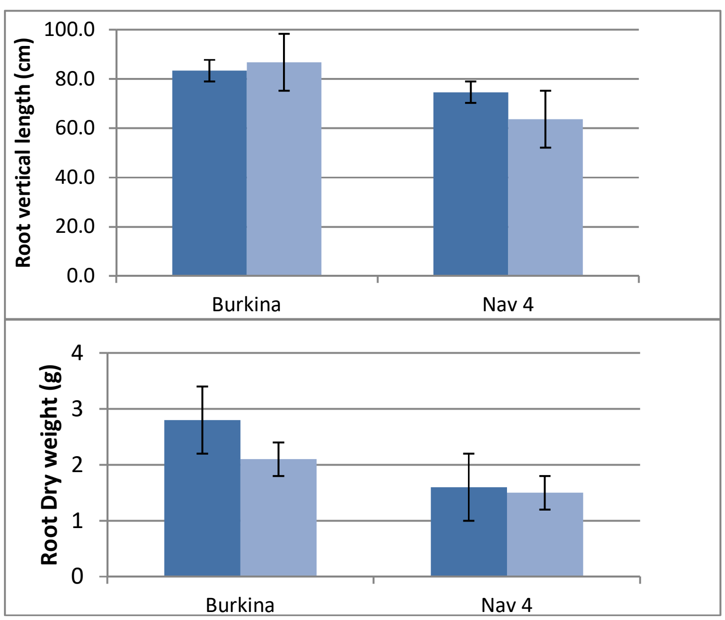


Figure 9.0. Final root vertical length and root dry weight of Burkina and Nav 4 landraces under watered (■) and drought (■) conditions. Bars represent mean values, means values ± standard deviation, n = 6.

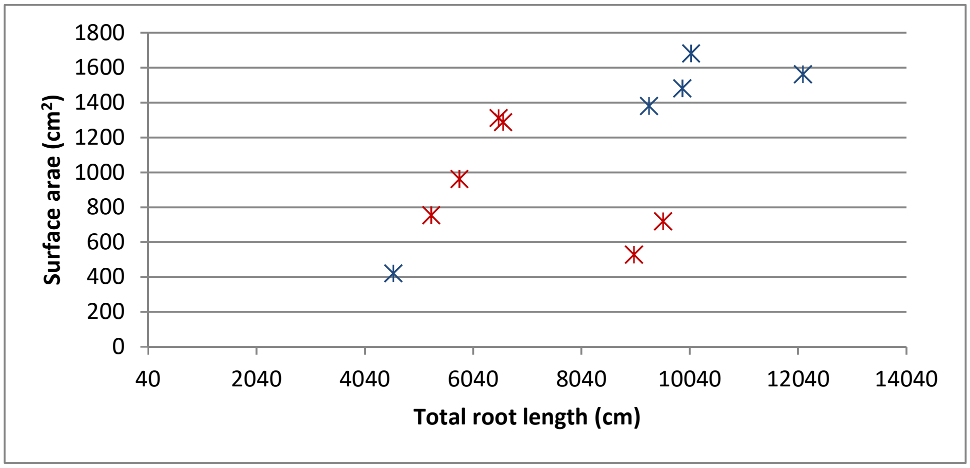


Figure 10.0. Final surface and total root length of Burkina (⁎) and Nav 4 (⁎) landraces under drought conditions. N= 6.

Table 3.0 Final total length, projected area, surface, average diameter and vertical length of roots of Burkina and Nav 4 landraces under watered conditions.

	Plant number	Total length (cm)	Projected area (cm^2)	Surface area (cm^2)	Average Diameter (mm)	Vertical length (cm)
Burkina	1	4564.39	134.01	420.99	0.29	59
	2	12129.70	497.03	1561.47	0.76	100
	4	9901.78	471.28	1480.59	0.48	96
	5	9282.62	439.82	1381.75	0.47	93
	6	10062.64	535.38	1681.94	0.53	86
Nav 4	1	5782.86	306.36	962.45	0.53	71
	2	9544.95	409.72	1287.17	0.43	61
	3	6507.02	228.90	719.12	0.35	52
	4	9006.75	417.28	1312.30	0.46	60
	5	5261.12	167.96	527.65	0.32	65
	6	6588.96	240.34	755.04	0.36	73

Table 4.0 Final total length, projected area, surface, average diameter and vertical length of roots of Burkina and Nav 4 landraces under drought conditions.

	Plant number	Length (cm)	Projected area (cm^2)	Surface area (cm^2)	Average Diameter (mm)	Vertical length (cm)
Burkina	1	7550.32	288.30	905.72	1.08	94
	2	9367.87	385.06	1209.71	1.12	62
	3	14316.20	827.37	2599.27	1.15	86
	5	7243.36	507.75	1595.15	0.70	80
	6	14636.20	673.54	2115.90	0.92	95
Nav 4	1	7787.73	413.98	1300.54	0.53	73
	2	3639.74	123.19	387.00	0.34	55
	3	7421.95	342.16	1074.91	0.46	68
	4	4467.46	166.86	524.20	0.37	74
	5	6004.01	260.94	819.78	0.43	90
	6	8115.33	445.23	1398.72	0.55	88

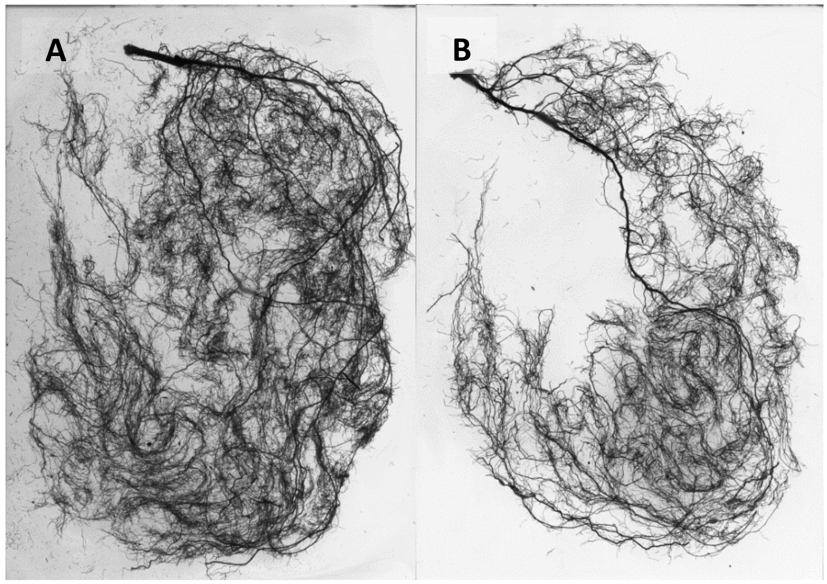


Image 4.0. Roots of Burkina (A) and Nav 4 (B) under drought conditions at final harvest.

3.4 Discussion

Results indicate a number of key differences between the two landraces. There was no significant change in chlorophyll content in response to drought as has been found in other studies (Vuragai *et al.,* 2011; Mabhaudi *et al*., 2013) suggesting Bambara groundnut can maintain chlorophyll content when under stress. Between the two landraces however, Burkina had significantly higher chlorophyll content under irrigated conditions and overall seemed to allocate more resources into biomass production, as reflected in the increase plant height, leaf number and canopy spread. It appears that while Burkina dedicated more resources to plant biomass production, Nav 4 was much quicker to produce pods and had fewer leaves, lower chlorophyll content and plant height. Under irrigated conditions there was no significant difference in final pod yield; however in the drought treatment Nav 4 produced significantly more pods. This is possibly as a result of its faster development rate and the fact that it began pod formation before the onset of drought, whereas Burkina took longer to progress through its reproductive stages and focussed instead on plant growth. In drought-prone climates, a faster rate of development may be a useful approach to ensuring yield stability as plants are able to produce yields before water stress takes effect. While in this case it seems that Nav 4 performed better in terms of yield potential, it is difficult to determine the real responses to water stress. This is because the drought treatment was imposed late in the plant's life cycle and may not have been imposed long enough to induce a sufficient enough response in the landraces. At the same time, some Nav 4 plants showed signs of heat stress before and during the drought treatment due to high soil temperatures, which is likely to have affected results.

Results from root analysis identified more clear differences between the landraces. Burkina had significantly longer root lengths in the drought treatment, significantly greater surface area in the irrigated treatment and greater root dry weight in the drought treatment than Nav 4. Although not significantly different, average Burkina root vertical length increased in response to drought whilst Nav 4 showed a slight reduction. This possibly reflects a greater deep rooting capacity of Burkina plants to capture more water during water stress further into the soil profile at the cost of reducing total surface area. A higher taproot length may have helped Burkina plants maintain above ground biomass production for longer, however it seems this was also done at the expense of pod production. Increased taproot length is a well-documented root response to water stress (Comas *et al.*, 2013). Ideally a crop capable of withstanding periods of drought must be able to improve water uptake from the soil via increased root growth without compromising final pod yield. Further studies are needed in this area to properly determine the behaviour of these landraces in more

3.5 Conclusions and recommendations

Burkina and Nav 4 have in this trial demonstrated the different responses of Bambara groundnut landraces in response to drought. While these landraces have behaved differently, more work is needed to properly determine this behaviour under more rigorously controlled conditions. Higher soil and column temperatures, possibly a result of issues in column preparation, seem to have caused heat stress in some of the Nav 4 plants and affected plant growth. Both landraces demonstrated traits that are useful in developing drought tolerant varieties of Bambara groundnut, namely the seemingly fast development rate of Nav 4, and the greater rooting depth of Burkina. However, these findings cannot be said to be conclusive and further work is needed. It is suggested that in future work drought treatments should be imposed earlier and for a longer period of time, in order to capture to true extent of plant responses and paint a clearer picture of the most important traits.

4 METABOLIC AND PHYSIOLOGICAL TRAITS ASSOCIATED WITH BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA* (L.) VERDC) ADAPTATION IN IRRIGATED AND DROUGHT CONDITIONS

4.1 Introduction

An underutilised crop in which interest has increased in recent years is the African grain legume Bambara groundnut (*Vigna subterranea* (L.) Verdc). It is grown mainly by resource-poor farmers throughout sub-Saharan Africa, is highly nutritious and contributes to soil fertility. There is strong evidence that bambara groundnut is more drought tolerant than many other legumes (Linnenmann and Azam-Ali, 1993), however the underlying mechanisms are not fully understood (Ntundu, 1997). Identifying these processes involved is essential if the potential of this crop is to be unlocked.

Research suggests certain physiological and metabolic traits contribute to the plant's resilience, namely a reduction of transpiration by stomatal control, a high root: shoot biomass ratio, maintenance of leaf turgor, an increase in partitioning of dry matter to roots and a reduction in leaf area development (Collinson, 1996; Collinson *et al.*, 1997). In the former of these two studies, plants which were subjected to drought from 35 days after sowing (DAS) were still able to produce some yield, which contrasts with work done on groundnut (*Arachis hypoganea*) where in similar conditions no pods were produced at all (Babiker, 1989).

Few studies have attempted to identify the response of Bambara groundnut genotypes specifically to temperature stress, but those that have reveal useful initial insights. Berchie *et al.,*(2012) evaluated the response 5 landraces of Bambara groundnut to temperatures ranging from 34.7 to 38.7 °C. As temperatures exceeding 38°C, pod yield was negatively affected even though irrigation was provided. Nevertheless, the landrace Burkina from Burkina Faso, proved to be the most drought tolerant landrace and still managed to produce pods at high temperatures whilst other landraces produced none. The landrace Burkina has also demonstrated considerable tolerance to drought and heat stress in other studies (Opoku, 2010). Al-Shareef *et al*., (2014) found that during high temperatures and under moderate drought, the landrace S19-3 produced significantly higher pod yields than Uniswa Red.

Despite these benefits, there is considerable evidence that Bambara groundnut is particularly susceptible to drought during late flowering and the pod filling stages. Studies that investigated this have found that when drought occurs during vegetative or early flowering, plants are able to recover and produce some yield, yet when imposed later, landraces are largely unable to do so (Jørgensen *et al*., 2011). It is possible that in legumes, water deficit during flowering can hinder the development and fertilisation of the stamen, resulting in loss of pollen and ultimately reduced seed production (Thuzar *et al*., 2010). Some varieties of cowpea (Vigna unguiculata L.), have also been shown to be susceptible to drought during early vegetative stages (Mai-Kodomi, 1999a).

Work by Mwale et al*.,* (2007) observed that landraces responded to drought through reductions in canopy size and leaf area expansion, as well as total dry matter and pod dry matter. Differences in rates of growth amongst landraces were identified which play an important role in drought tolerance. For example, the S19-3 landrace, which is from an environment characterised by low rainfall and a short growing season, performed better under drought conditions than Dip C and Unisa-red which are from regions of higher rainfall and a longer growing season. The greater yields shown in S19-3 were attributed to its faster rate of growth and development, with yield formation occurring much sooner than the other landraces and has been shown in other studies (Karunaratne *et al*., 2010). These differences demonstrate the range of characteristics that exist among landraces that can be of use in crop management and for the selection of traits in breeding programmes. Such findings highlight the need to better understand the underlying mechanisms and traits can confer these differences. Further, yields found this study (1.65 t ha^{-1}) were on average higher than what has been reported from cowpea (0.3-0.5 t ha^{-1}) under similar conditions (Leport *et al.,* 1999), further underscoring the value of this crop.

One area in particular that has received relatively little research attention so far is the behaviour of roots of Bambara groundnut in response to periods of drought. While increased root biomass has been identified in some studies, the specific root traits that are associated with drought tolerance are yet to be identified, as well as the differences in root characters between contrasting landraces. Considering the central role roots play in plant water relations, investigating these traits is essential in efforts to understand the nature of Bambara groundnut's drought tolerance. Work by Mwale *et al*., (2007) found that under drought conditions roots were up to 40m longer than those under irrigated conditions and an a high root to total dry matter ratio, which was also shown in earlier studies (Collinson, 1996). In intercropping studies it has been shown that when grown alongside rice, Bambara groundnut occupies greater soil volume and shows a higher root density (Andika *et al*., 2010). This indicates capacity to increase root growth to obtain water and minerals when under stress or under competition with other plants.

As well as the physiological effects of water deficit, metabolic processes are also greatly affected. Changes in cells, such as the thickening of cell walls, are amongst the anatomical changes that can occur in plants in response to water stress *(reference to follow).* Compounds and other solutes can accumulate which increase the osmotic potential within the cell which in turn restricts water loss through osmosis (reference to follow). One such osmolyte is the amino acid proline, which has been seen in several species to increase in response to drought and can therefore be a useful measure of water stress (Abdalla and El-Khoshiban, 2007; Hare and Cress, 1997). Studies with Bambara groundnut have generally shown their accumulation during periods of drought, however further investigation is needed in this area (Vurayai *et al*., 2010*)*.

Another group of compounds which are used as indicators of various environmental stresses are the anthocyanin pigments. Belonging to the flavonoid family, these water-soluble pigments are located in the vacuoles of mesophyll and epidermal cells and are thought to have roles in protection against various stresses, including ultraviolent radiation and drought (Hatier & Gould 2008). Although not explored in Bambara groundnut research, anthocyanins have been shown to play some role in osmotic induction and studies have demonstrated increased accumulation under drought conditions in various species (Chalker-Scott, 1999).

Considering the great diversity of Bambara groundnut landraces, much more work is needed to explore the differences between contrasting landraces to be better understand the role of these mechanisms.

4.1.1 Objectives

The objectives of this experiment were to assess the impact of drought on root parameters, plant development, chlorophyll content, stomatal conductance and leaf anthocyanin concentration of landraces of Bambara groundnut.

4.2 Methodology

4.2.1 Site and Materials

This trial took place at the University of Nottingham Malaysia Campus in Semenyih, Malaysia, from March to August of 2015. Three landraces of Bambara groundnut (summarised in table 1.0) were grown under irrigated and drought conditions in a screen house on campus, the walls of which are made from plastic mesh allowing for ventilation and light to pass through. The soil used was a sandy loam soil, which was brought to the shade house from the Field Research Centre and had a pH of 4.2. Seeds were sown on 18th March 2015 in PVC soil columns which were 120cm in height and 20cm in diameter and consisted of two sections attached together with scotch packaging tape (see image 5.0). Soil columns were chosen as the medium for growing plants as they provide a more realistic growing environment than pots and allow for greater rooting depths. Each column was filled with 50kg of soil and watered to field capacity and allowed to drain before sowing seeds. Three seeds were sown per columns which were then thinned to one plant per column four days after seedling emergence.

Image 5.0. The screen house (left) and soil columns

Landrace	Origin	Seed Colour
TVSU89	Mali (also grown in Thailand)	Cream
Mana	Zimbabwe	Red
Getso	Nigeria	Cream

Table 5.0. Bambara groundnut landraces

4.2.2 Treatment and Design

The experiment was arranged as a completely randomised design with 4 replicates and two treatments (watered and drought), largely due to the relatively small number of columns used. The control plants were well watered every other day by hand to roughly 50% field capacity of the soil throughout the experiment, whereas plants in the drought treatment received the same irrigation regime up until 28th May (71 days after sowing) after which no further irrigation was applied for 5 weeks. This period was chosen for the onset of drought as it coincided with late flowering; a stage which Bambara groundnut appears to be particularly vulnerable to water stress (Vurayai *et al*., 2011; Jørgensen *et al*., 2011). This irrigation regime was also chosen due to the high sensitivity of Bambara groundnut to waterlogging and the high-water retaining capacity of the soil used in this experiment. Further, 5 weeks was chosen to provide sufficient time for water stress to occur in the columns whilst not being so severe as to result in complete loss of plants.

Data was analysed using Genstat statistical software version 14, in order to carry out the Student's t-tests. T-Tests were used largely due to the smallness of the sample size as a result of the loss of replicates in the course of the experiment (explained in the following section).

4.2.3 Procedure

Each column was subject to fertiliser treatments two weeks before sowing, including nitrogen, phosphorous and potassium inputs in the form of urea, single superphosphate and muriate of potash. Plant emergence was measured on all plants starting from 6 DAS until full emergence was achieved, which was recognised as when seedlings showed 90% emergence. After full emergence, plant height, leaf number, leaf size, soil moisture content, chlorophyll content, stomatal conductance and anthocyanin concentrations were measured at various stages.

Three columns of each landrace for both treatments had circular apertures cut at 3 different points along the column profile: 20cm, 50cm and 80cm. Each aperture was covered by tape and a piece of PVC that can be hinged open like a door (see image 6.0). In order to periodically measure the soil moisture content, a Theta-T probe (ML2x Delta T Devices, Cambridge, UK) attached to a Moisture Meter (HH2 Delta T Devices, Cambridge, UK) was inserted into the soil at the surface (0cm) and 20cm, 50cm and 80cm via the apertures. The probe measures volumetric soil moisture content which is the ratio between the volume of water and the volume of the soil sample and is expressed as a percentage volume (%).

Image 6.0. The apertures on the columns (left) and the inserted soil moisture probe (right)

Chlorophyll content was measured weekly on each plant using a SPAD-502 chlorophyll meter. Readings were taken from the abaxial side of three young but fully expanded leaves per plant to represent the average. Each measurement was taken from 9:00am.

Stomatal conductance measurements were taken using a leaf Porometer, Decagon Devices. Due to the rising rate of transpiration (and consequently stomatal opening) throughout the morning, it was essential to complete all measurements as soon as possible. For that reason, stomatal conductance measurements were taken first to minimise the effect of rising temperatures and increasing sunlight.

Anthocyanin measurements were taken weekly using the ACM-200*plus* anthocyanin metre. The metre allows for rapid and non-destructive measurements of anthocyanin content in intact leaves by measuring energy absorbed at two wavebands, which produces an anthocyanin content index (ACI) reading. This method was used to obtain anthocyanin concentrations from each plant and an effort was made to avoid placing the cuvette on the veins of the leaves as this can influence the readings.

Half way through the treatments, an accident occurred whereby an unstable column collapsed and caused a further dozen to collapse. Only three of the plants were fully recovered, resulting in significant loss of replicates for both treatments. It was then decided that rather than leave some plants to grow post-harvest to assess recovery and obtain seeds, all plants would be harvested after the 5 weeks to obtain as much data as possible. Once the treatment period came to end, leaves, stems and any pods were removed and separated into paper bags before being placed into a fridge to preserve for analysis. Immediately after this was done, roots were harvested by placing the columns on the ground, breaking the tape holding the two pieces together and then carefully washing off the soil using a hose pipe. The roots were then placed in sealable zip lock bags and then similarly placed in the fridge before further analysis. Leaves were put through a leaf area metre (LI-3100 Area Meter, LI-COR) to measure leaf area index and then were weighed using an electronic weight, along with the shoots, to measure fresh dry weight. Subsequently, leaves and shoot were placed in an oven heated to 80°C for 48 hours and then re-weighed to obtain dry weights. Fresh weights were likewise taken for roots, before undergoing root scanning, for which samples were then taken to the lab and washed to remove dirt, stones and other organic matter present in the soil. Images of roots were generated and analysed by the root imaging software WinRHIZO. Upon completion of root scanning, roots were then placed in the oven for 48 hours and re-weighed to obtain dry weights. An example of the analysed root images can be seen in image 3.0 below.

4.3 Results

4.3.1 Field Measurements

From physical observations, it was noticed that general greeness of the plants did not change in the first 2 weeks and there was no visible difference between the landraces. This is reflected in the leaf chlorophyll content, which decreased in all landraces after roughly 4 weeks.

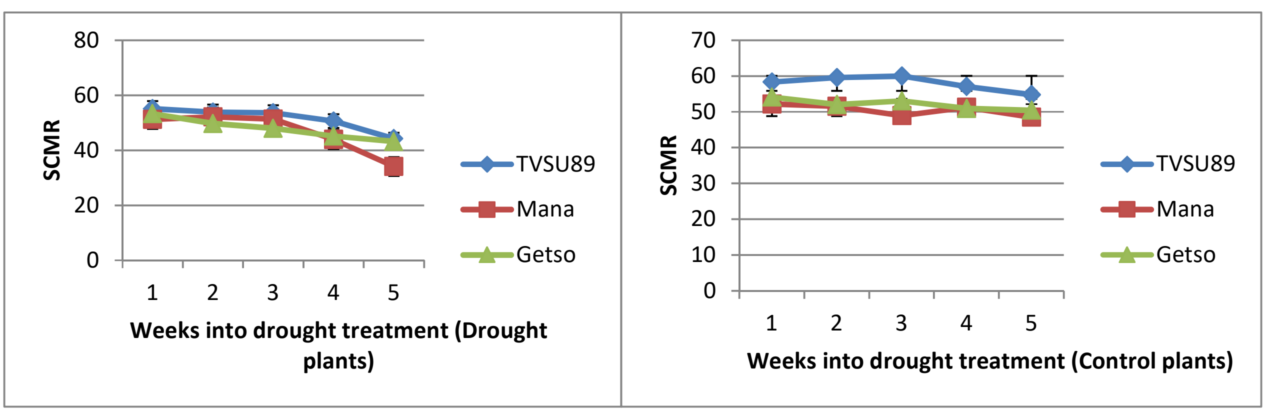


Figure 11.0 SPAD chlorophyll meter readings (SCMR) of landraces of Bambara groundnut under drought and irrigated conditions. Error bars represent standard deviation. N = 6.

TVSU89 maintained the highest chlorophyll content for both treatments and was significantly higher than Mana at the end of irrigation (P<0.005) but not significantly higher than getso (p>0.05). Mana had the lowest content in the drought treatment after 5 weeks.

Stomatal conductance decreased in all landraces after 4 weeks of drought and after 5 weeks there was a significant difference between the two treatments for all landraces.

TVSU89 maintained a significantly higher stomatal conductance than both landraces at the end of the drought treatment (P<0.05).

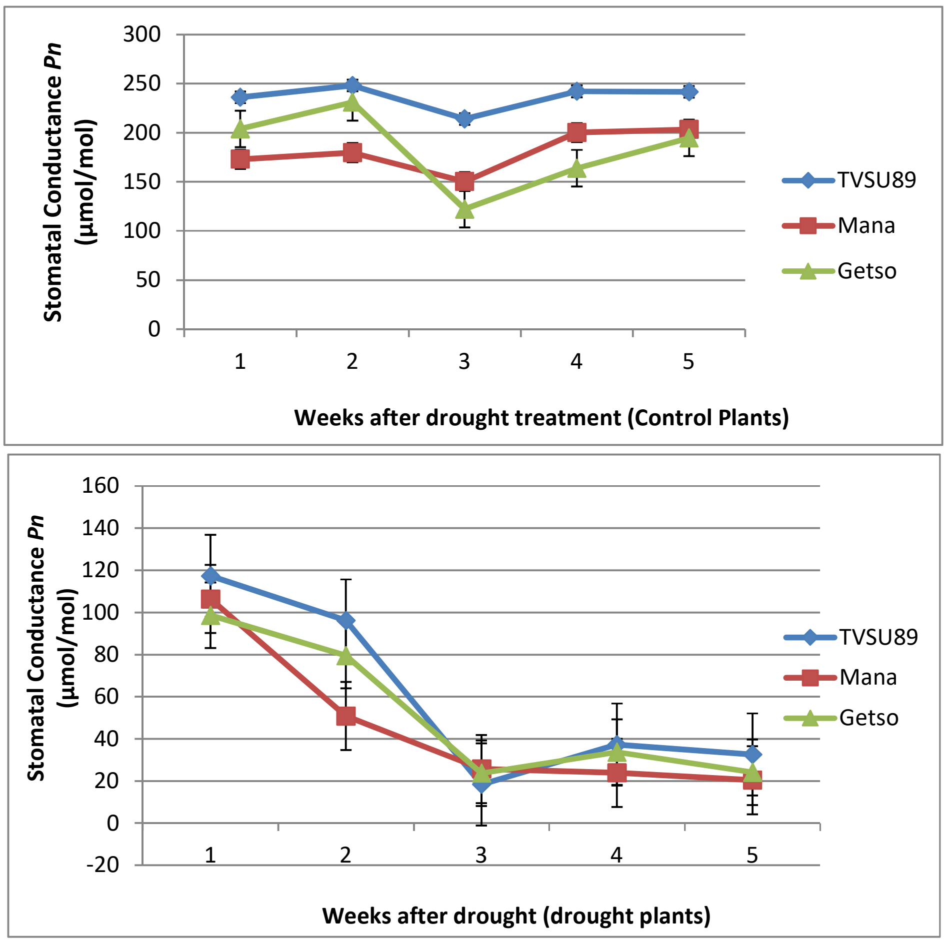


Figure 12.0. Stomatal conductance of landraces of Bambara groundnut under drought and irrigated conditions. Error bars represent standard deviation.

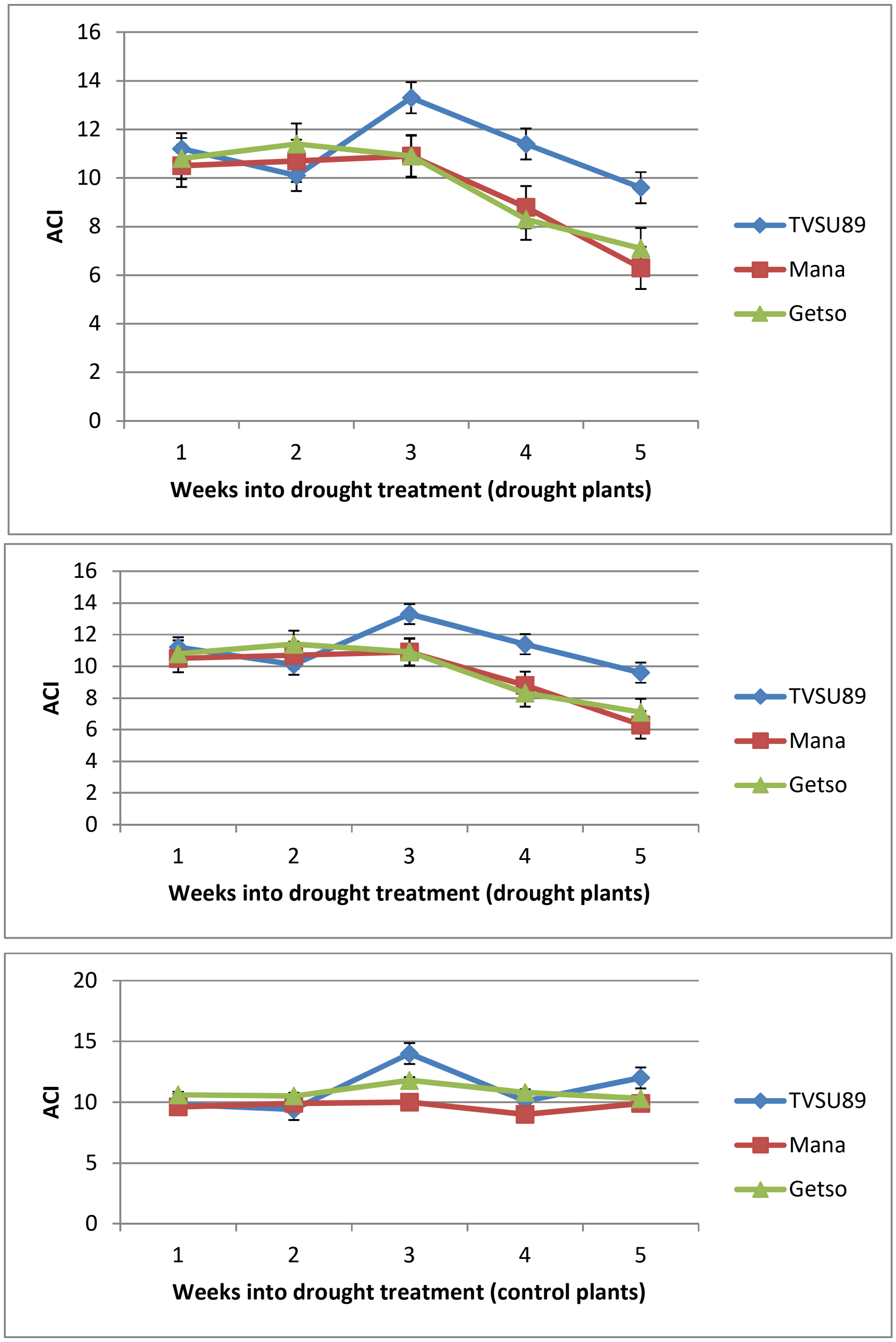


Figure 13.0. Anthocyanin content index (ACI) of landraces of Bambara groundnut under irrigated and drought conditions

Anthocyanin concentrations were higher under irrigated conditions; drought induced a reduction in anthocyanin concentration in all landraces. Both mana and getso had significantly lower anthocyanin concentrations under drought conditions ($p<0.05$ and 0.01 respectively) but not TVSU89 which maintained significantly higher anthocyanin concentrations than Mana and Getso (p>0.05).

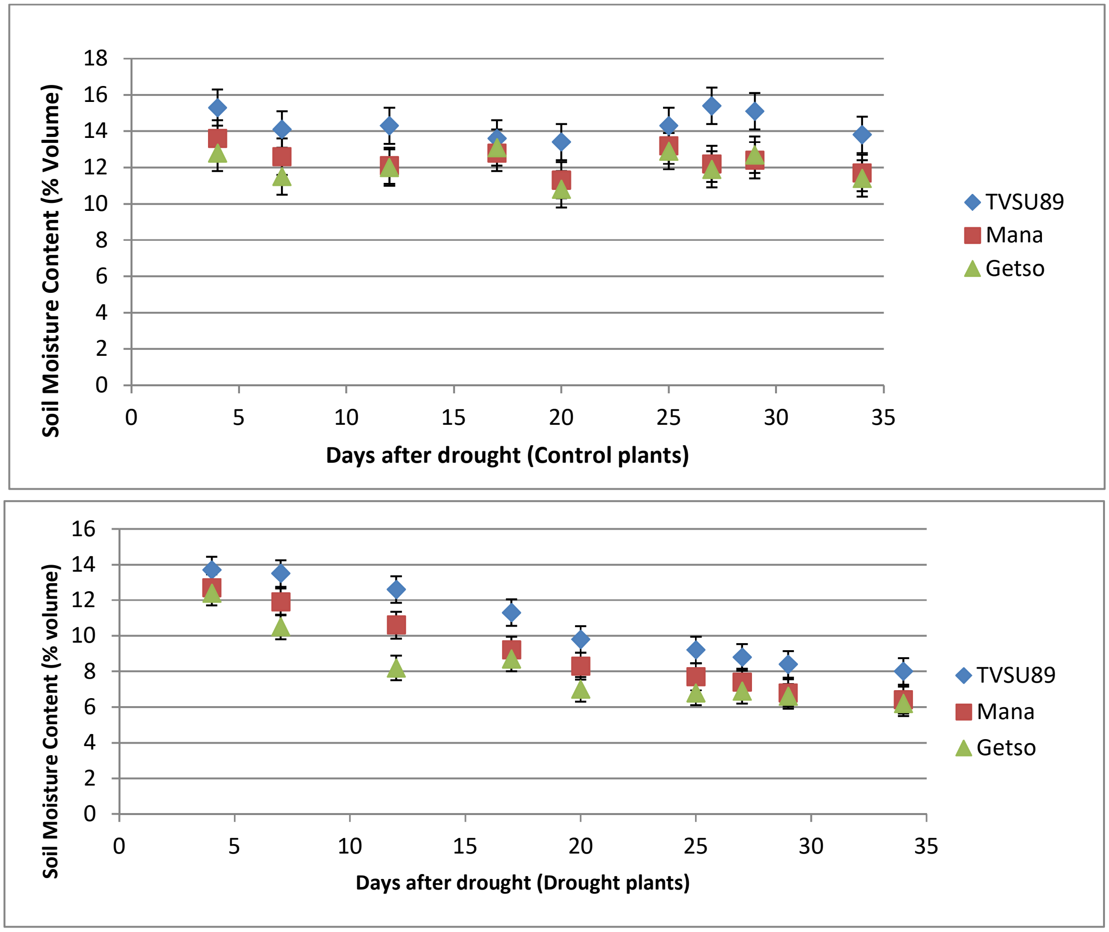
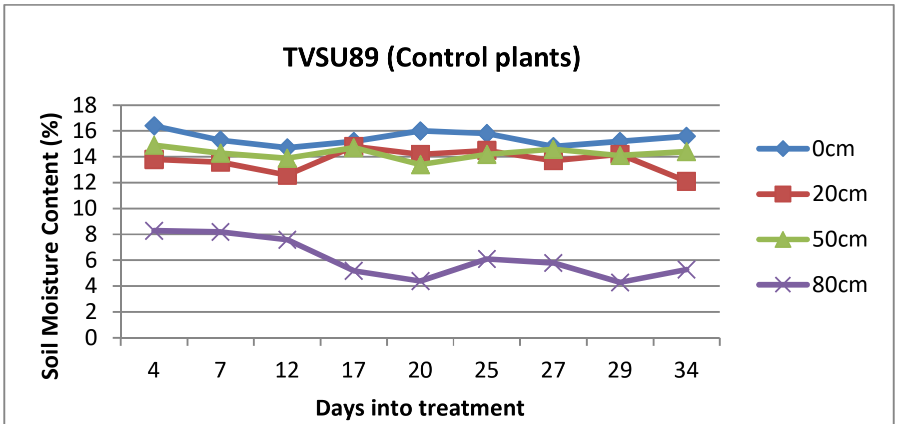
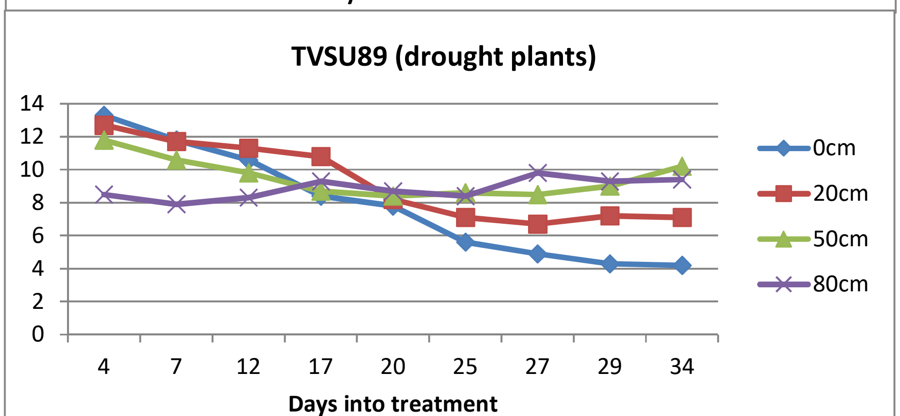


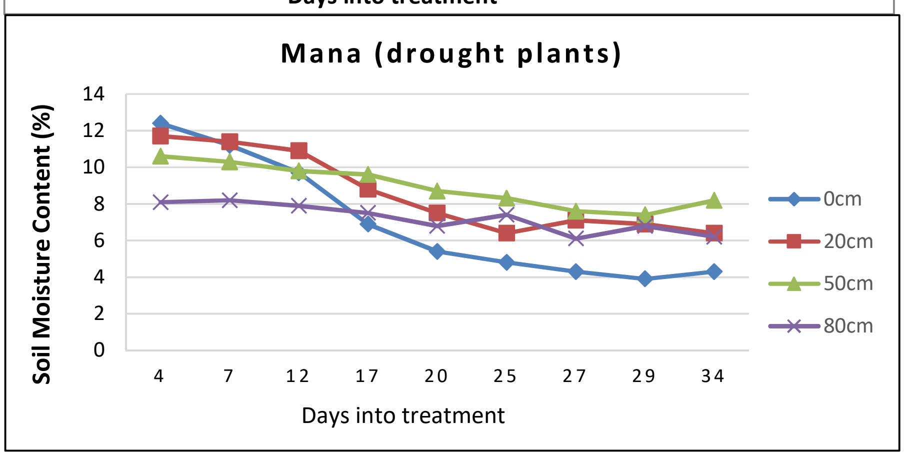
Figure 14.0. Soil Moisture Content at soil surface for landraces of Bambara groundnut under drought and irrigated conditions.

Due to the loss of several columns which were used for investigating soil moisture content, there is little valid data that can be used for a proper analysis. Nevertheless, some general trends can be ascertained. By day 12 there was a noticeable drop in the soil moisture content at the soil surface in most plants in the drought treatment. This drop was most apparent in Getso which also consistently had the lowest soil moisture content in all treatments.

In the drought treatments for all landraces there was a general trend of a rapid decline in soil moisture content at 0cm, 20cm and 50cm whilst it remained relatively constant at the bottom of the column at 80cm.







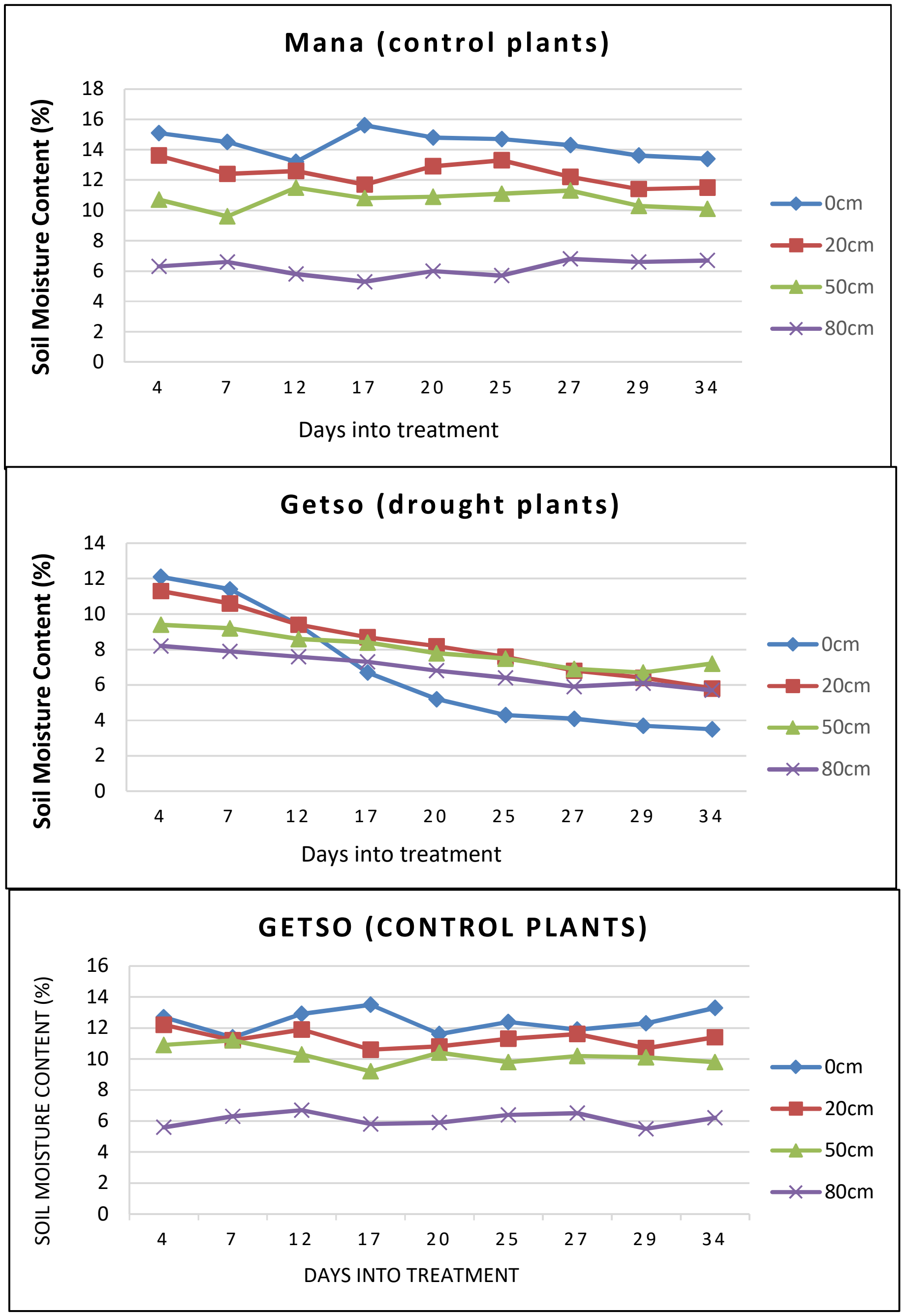


Figure 15.0. Soil moisture content at different points in the soil profile among landraces of Bambara groundnut in irrigated and drought conditions

Leaf number overall decreased in the drought treatment. Under drought conditions mana plants saw an average of a 47% decrease in leaf number which was significantly lower than under irrigated conditions ($p<0.01$). Similarly, Getso plants had an average of 57% fewer levels in the drought treatment and saw the greatest leaf reduction ($p<0.05$). In TVSU89 plants, there was an increase in leaf number during the third week of drought and although it then decreased it remained significantly higher than the other landraces ($p<0.05$) (see figure 16.0).

TVSU89 also had highest leaf number in the irrigated treatment ($P<0.05$).

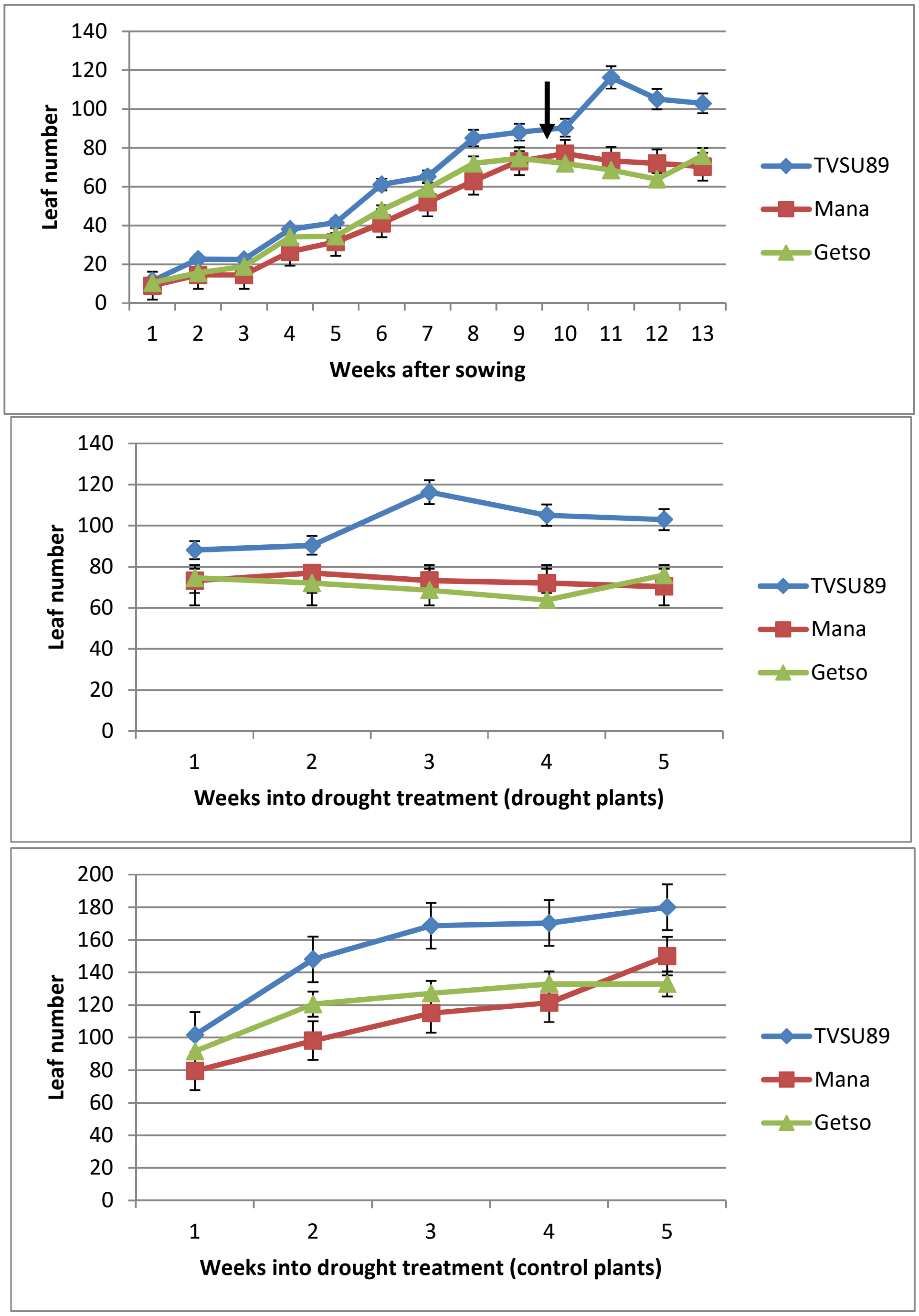


Figure 16.0. Leaf number of landraces of Bambara groundnut landraces under drought and irrigated conditions. Arrow represents beginning of drought treatment.

4.3.2 Post-Harvest Results

Leaf and shoot fresh weight were significantly reduced in all landraces in the drought treatment ($p<0.05$). In both treatments, TVSU89 had the lowest leaf dry and fresh weights, however this was not significantly higher ($p>0.05$). Mana had the highest leaf and shoot dry weights for both treatments.

Root fresh weight did not significantly reduce in drought conditions in TVSU89 or mana ($p>0.05$) however it did in getso plants ($p<0.05$). Getso plants also had the highest root fresh weight but this was not significantly higher than the other landraces ($p>0.05$). Root dry weight showed no significant reduction for any landrace ($p>0.05$) (appendix table 35).

TVSU89 had highest pod number in control treatment (42) and was the only landrace to produce pods in drought treatment (2). Overall pod yield was poor in both treatments.

LAI decreased significantly in all landraces at the end of drought ($P<0.05$). There were no significant differences between landraces, however under watered conditions TVSU89 had lowest leaf area index and Mana had the highest at the end of the drought treatment (see figure 17.0).

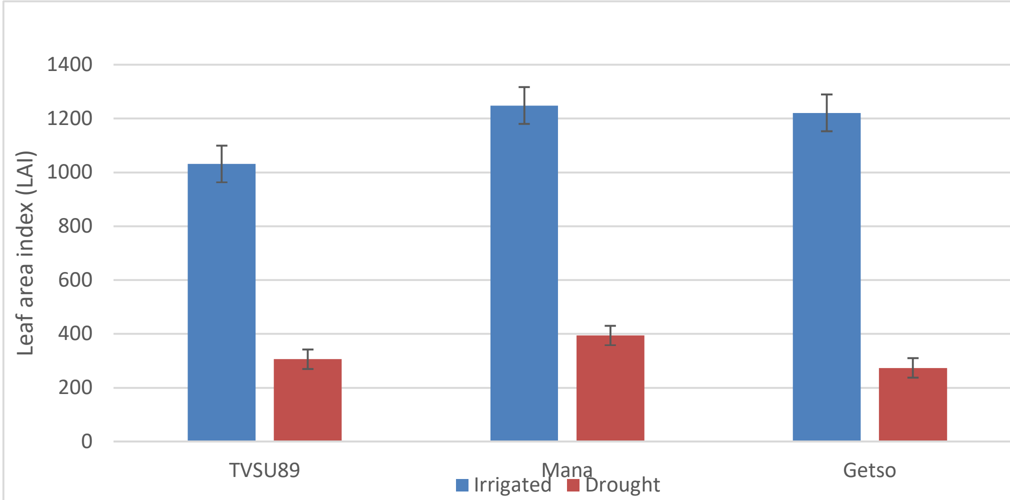


Figure 17.0. Leaf area index (LAI) of landraces of Bambara groundnut under irrigated and drought conditions

4.3.3 Root parameters

Root length per volume decreased in drought treatment for all landraces (see figure 18.0). There was a significant decrease for mana and getso (P<0.05) but not TVSU89 (P>0.05).

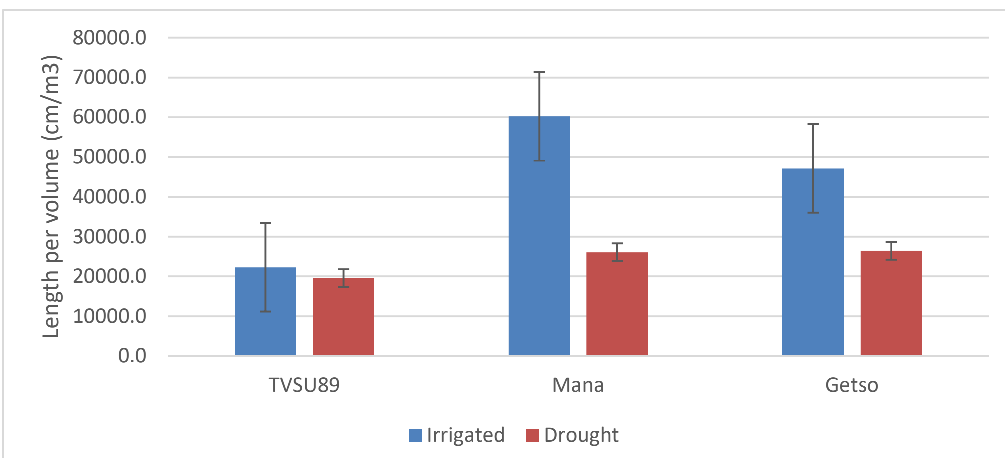


Figure 18.0. Root length per volume of landraces of Bambara groundnut under irrigated and drought conditions

Root surface area decreased in drought treatment for all landraces. This was not a significant decrease for TVSU89 or Getso, however Mana plants showed a significant decrease (see figure 19.0).

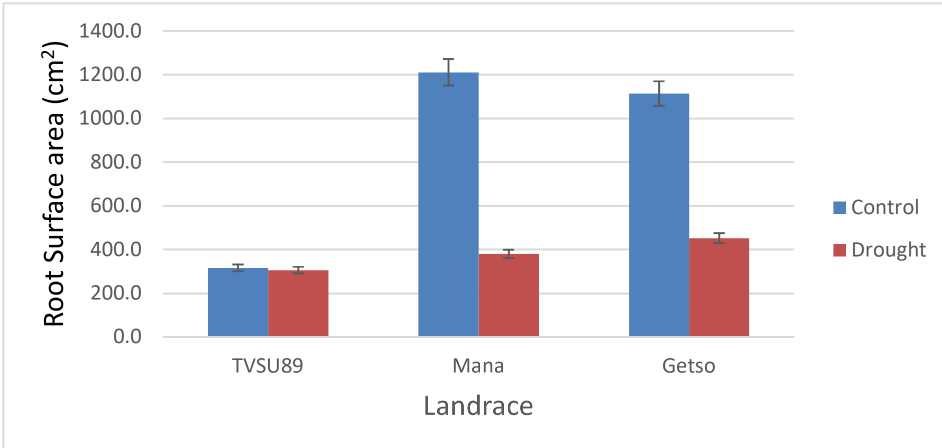


Figure 19.0. Root surface area of landraces of Bambara groundnut under irrigated and drought conditions

TVSU89 showed an increase in root diameter in the drought treatment, whereas mana and getso exhibited a reduction. The number of root tips also decreased in all landraces in the drought treatment with getso having the highest number. In the irrigated treatment Mana had the greatest number and getso had the lowest. Fork number also reduced across all landraces in the drought treatment, with TVSU89 having the lowest number in both treatments (appendix table 37).

4.4 Discussion

The primary purpose of this experiment was to identify physiological and metabolic responses of Bambara groundnut landraces to water stress. Due to the relatively small sample size, partly due to the incident which resulted in the loss of several columns, the main source of insight can be derived from ways in which the landrace TVSU89 differed from the other Mana and Getso.

Overall TVSU89 showed the greatest final pod yield in both treatments which could potentially linked to several key traits. TVSU89 had the lowest leaf fresh and dry weights, which may be an indication of a strategy to avoid drought as observed in other studies by reducing plant growth and prioritising pod yield (Mabhaudi *et al.* 2013). However, all roots in the drought treatment, including those of TVSU89, displayed a reduction in length and surface area. This contrasts with suggestions of previous studies that increasing the partitioning of dry matter to roots is a potential strategy of Bambara groundnut to tolerate drought (Babiker, 1989; Collinson *et al*., 1997). TVSU89 also already had a much lower root length and surface area under irrigated conditions, which may indicate it is capable of early maturity and therefore able to avoid terminal drought. There may also be a trade-off between root growth and pod production; the latter being the priority for the landrace TVSU89. In other studies, a reduction in root dry weight has been observed in response to drought which suggests a possible drought tolerance strategy (Muhammad *et al.,* 2016). Getso has also been shown to be a drought tolerant landrace, a possible indication of a link between the environmental origins of a landrace and its ability to withstand water stress (Muhammad *et al.,* 2016). Nevertheless, further research on the development of roots of the landrace TVSU89 would be needed to explain this apparent contradiction in findings.

Another previously identified strategy of drought tolerance is reducing stomatal conductance (Collinson *et al*., 1997), which the findings of this investigation can support. All landraces saw a reduction in stomatal conductance in the drought treatment, however it was TVSU89 that maintained a higher stomatal conductance than the other landraces. The higher stomatal conductance may be attributed to the ability of TVSU89 to maintain a greater rate of photosynthesis which allows it to maintain a higher chlorophyll content, and therefore ensure a reliable pod yield. Further, TVSU89 had a higher anthocyanin content under drought conditions than both mana and getso. Maintaining its metabolic activity in this way may explain in part the capacity of TVSU89 plants to maintain photosynthesis in drought conditions (Tezara *et al*., 1999). Exploring the size and thickness of leaves would provide further insight into the way landraces maintain sufficient photosynthetic processes under water stress (Liu *et al*., 2004).

Production of anthocyanin has been linked to the maintenance of protein conformation at low moisture levels and reducing photodamage (Reddy *et al*., 2004; Efeoğlu *et al*., 2009). It has been suggested that an increase in anthocyanin production under water stress is linked to the photoprotection of chlorophyll (Garriga *et al.*, 2014), which may explain the maintenance of chlorophyll in TVSU89 in this investigation. Interestingly, Chirabada *et al.,* (2015) found no difference in chlorophyll content among landraces of Bambara groundnut in different water regimes. There are indications that metabolic processes may enable drought tolerant landraces to maintain good pod yields under water stress and so further investigation in this area is necessary.

Water use efficiency was an area that was not the focus of this study, however there are indications that this has played a role in tolerance of water stress. For example, TVSU89 plants consistently had a greater soil moisture content at the soil surface level. This may suggest that TVSU89 has a greater water use efficiency, which is a function of reduced water use and improving plant production (Blum, 2005).

Although some general trends have been identified, there were several limitations to this investigation which demand further research. Apart from the loss of several columns, thereby significantly compromising the available data, issues with the growing conditions may have also influenced the findings. For example, the shade house in which the plants were grown had a very high day temperature and relative humidity which may have affected stomatal conductance and other physiological responses (Sanchez-Blanco *et al*., 2004). However, due to the lack of a fully functioning temperature probe, it is not possible to determine what the temperature and humidity were and therefore suggest the potential effect it may have had on the results. Nevertheless, this investigation demonstrates the clear potential for using column-based methods to investigate the development of roots in response to drought in Bambara groundnut and has successfully identified some potential root parameters which merit further investigation.

4.5 Conclusion

This investigation has identified some key potential parameters for drought tolerant strategies in Bambara groundnut. These include a reduction in leaf and shoot biomass, increased production of metabolites such as anthocyanin, a reduction in stomatal conductance, maintenance of chlorophyll content. While root volume and surface area reduced under drought conditions, this may be attributed to maximising photosynthetic capacity to ensure pod production.

A column-based method to investigate root responses has the potential to identify the differences between landraces of Bambara groundnut. Further studies should include a wider range of landraces from various climatic conditions, which can be more thoroughly examined at different stages of development. Further, column-based methods would benefit from growing conditions that are more rigorously controlled, to enable clear links between these physiological and metabolic traits to be identified.

REFERENCES

Al Shareef I, Sparkes D, Azam-Ali S (2013). Temperature and Drought Stress Effects on Growth and Development of Bambara Groundnut (*Vigna subterannea* L.) *Experimental Agriculture* **50**: 72-89.

Andika DO, Abukutsa-Onyango MO, Onyango JC, Stutzel H (2010). Roots Spatial Distribution and Growth in Bambara Groundnuts (*Vigna subterranea*) Intercrop System. *ARPN Journal of Agricultural and Biological Science* **5:** 39-50.

Azam-Ali SN, Sesay A, Karikari SK, Massawe FJ, Aguilar-Manjarrez J, Bannayan M, Hampson KJ (2001). Assessing the Potential of An Underutilized Crop – A Case Study Using Bambara Groundnut. *Experimental Agriculture* **37:**433-472.

Babiker AMA (1989). Growth, dry matter and yield of bambara groundnut (*Vigna subterranea*) and groundnut (*Arachis hypogaea*) under irrigated and droughted conditions. MSc thesis, University of Nottingham, UK.

Berchie JN, Opoku M, Adu-Dapaah H, Agyemang A, Sarkodie-Addo J, Asare E, Addo J, 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* **7**(2): 250-256.

Blum A (2005). Drought resistance, water use efficiency and yield potential- are they compatible, dissonant or mutually exclusive? *Aust. J. Agric. Res.* **56:** 1159–1168.

Chalker-Scott L (1999). Environmental Significance of Anthocyanins in Plant Stress Responses. *Photochemistry and Physiology* **70:** 1-9.

Collinson ST, Azam-Ali SN, Chavula KM, Hodson DA (1996). Growth, development and yield of bambara groundnut (*Vigna subterranea*) in response to soil moisture. *Journal of Agricultural Science* **126**:307-318.

Collinson ST, Clawson EJ, Azam-Ali SN, Black, CR (1997). Effect of soil moisture defecits on the water relations of bambara groundnut (*Vigna subterranea* L. Verdc.). *Journal of Experimental Botany* **48**:877-884.

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

Comas LH, Becker SR, Cruz VMV, Byrne PF, Dierig DA (2013). Root traits contributing to plant productivity under drought. *Front Plant Sci* **4:**1-16 doi: 10.3389/fpls.2013.00442.

Efeoğlu B, Ekmekçi Y, Çiçek N (2009). Physiological responses of three maize cultivars to drought stress and recovery. *South African Journal of Botany* **75:** 34-42.

Garriga M, Retamales JB, Romero-Bravo S, Caligari PD, Lobos GA (2014). Chlorophyll, anthocyanin, and gas exchange changes assessed by spectroradiometry in Fragaria chiloensis under salt stress. J Int Plant Biol. **56:**505-15.

Jørgensen ST, Liu F, Ouedraogo, Ntundu WH, Sarrazin J, Christiansen JL (2010). Drought Responses of Two Bambara Groundnut (Vigna subterranea L. Verdc.) Landraces Collected from a Dry and a Humid Area of Africa. *Journal of Agronomic and Crop Science* **196:** 412-422.

Jørgensen ST (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:**25-36.

Karunaratne AS, Azam-Ali SN, Al-Shareef I, Sesay A, Jørgensen ST, Crout NMJ (2010). Modelling the canopy development of bambara groundnut. Agric. *ForestMeteorol* **150:** 1007–1015.

Leport L, Turner NC, French RJ, Barr MD, Duda R, Daves SL, Tennant D, Siddique, KHM (1999). Physiological responses of chickpea genotypes to terminal drought in a Mediterranean-type environment. *European Journal of Agronomy* **11**: 279–291.

Linnemann AR, Azam-Ali SN (1993). Bambara groundnut (Vigna subterranea). In Underutilized Crops: Pulses and Vegetables, 13±57 (Ed. J. T. Williams). London: Chapman & Hall.

Liu F, Andersen MN, Jensen CR (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.

Liu F and Stutzel H. (2004). Biomass partitioning, specific leaf area, and water use efficiency of vegetable amaranth (*Amaranthus* spp.) in response to drought stress. *Scientia Horticulturae* **102:** 15–27.

Mabhaudi T, Modi AT, Beletse YG (2013). Growth, phenological and yield responses of a bambara groundnut (Vigna subterranea L. Verdc) landrace to imposed water stress: II. Rain shelter conditions*. Water SA* **39:** 191-198.

Mai-Kodomi Y, Singh BB, Myers O Jr, Yopp JH, Gibson PJ, Terao T (1999a) Two mechanisms of drought tolerance in cowpea. *Indian J Genet* **59**:309–316.

Muhammad YY, Mayes S, Massawe F (2016). Effects of short-Term water deficit stress on physiological characteristics of Bambara groundnut (Vigna subterranea (L.) Verdc.) *South African Journal of Plant and Soil* 33:51-58.

Mwale SS, Azam-Ali SN, Massawe FJ (2007) Growth and development of bambara groundnut (Vigna subterranea) in response to soil moisture – 1. Dry matter and yield. *Euro. J. Agron* **26:**345–353.

Mwale SS, Azam-Ali SN, Massawe FJ (2007). Growth and development of bambara groundnut (Vigna subterranea) in response to soil moisture. 2. Resource capture and conversion. *European Journal of Agronomy* **26**:354-362.

Nakabayashi R, Mori T, Saito K (2014). Alternation of flavonoid accumulation under drought stress in *Arabidopsis thaliana. Plant Signalling Behaviour* **9:** 1-3.

Ntundu WH (1997). Tanzania Country Report. Bambara groundnut [*Vigna subterranea* (L.) Verdc] Promoting the conservation and use of under-utilised and neglected crops. 9. Proceeding of the workshop on conservation and improvement of Bambara groundnut (Vigna subterranea (L.) Verdc.) 14 –16, 1995, Harare, Zimbabwe (Heller J., F. Begeman and J. Mushonga) Institute of Plant Genetics and Crop Plant Research.

Opoku MK (2010). Response Of Bambara Groundnut Landraces To Heat And Drought Stress In The Guinea Savanna And Transition Zones Of Ghana. MSc Thesis, Kwame Nkrumah University Of Science And Technology, Ghana.

Reddy A, Chaitanya KV, Vivekanandan M (2004). Drought-induced responses of photosynthesis and antioxidant metabolism in higher plant. *Journal of Plant Physiology* **161**: 1189-1202.

Sanchez-Blancoa MJ, Ferra'ndeza T, Navarrob A, Banon S, Alarco JJ (2004). Effects of irrigation and air humidity preconditioning on water relations, growth and survival of *Rosmarinus officinalis* plants during and after transplanting. *Journal of Plant Physiology* **161:** 1133–1142.

Tezara W, Mitchell VJ, Driscoll SD, Lawlor DW. (1999). Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature* 1401, 914–917.

Vurayai R, Emongor V, Moseki B (2011). Physiological Responses of Bambara Groundnut (*vigna subetteranea* L. Verdc) to Short Periods of Water Stress During Different Developmental Stages. *Asian J. Agric. Sci.* **3**:37-43.

Zhang J, Jia W, Yang J, Ismail AM (2006). Role of ABA in integrating plant responses to drought and salt stress. *Field Crops Research* **97:**111-119.

APPENDIX

Table 1: ANOVA table for stomatal conductance in both treatments for all landraces

Groups	*Count*	*Sum*	*Average*	*Variance*		
Control	11	2316.8	210.6182	429.8636		
Drought	9	232.2	25.8	31.5575		
ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	169080.9	1	169080.9	668.7304	0.000547	4.413873
Within Groups	4551.096	18	252.8387			
Total	173632	19				

Table 2: ANOVA table for stomatal conductance between TVSU89 and Mana plants at the end of the irrigation treatment

Groups	*Count*	*Sum*	*Average*	*Variance*		
TVSU89	3	725.4	241.8	23.56		
Mana	4	812.6	203.15	10.68333		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	2560.839	1	2560.839	161.7304	0.0000571	6.607891

Within Groups	79.17	5	15.834			
Total	2640.009	6				

Table 3: ANOVA table for stomatal conductance between TVSU89 and Getso plants at the end of the irrigation treatment

Groups	*Count*	*Sum*	*Average*	*Variance*		
TVSU89	3	725.4	241.8	23.56		
Getso	4	778.8	194.7	21.96667		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	3802.989	1	3802.989	168.2441	0.000485	6.607891
Within Groups	113.02	5	22.604			
Total	3916.009	6				

Table 4: ANOVA table for chlorophyll content in TVSU89 plants at the end of irrigated and drought treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	3	164.5	54.83333	8.803333		
Drought	3	132.9	44.3	0.63		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	166.4267	1	166.4267	35.28481	0.004028	7.708647
Within Groups	18.86667	4	4.716667			
Total	185.2933	5				

Table 5: ANOVA table for chlorophyll content in Mana plants at the end of irrigated and drought treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
irrigated	3	193.8	48.45	0.596667		
drought	4	102.2	34.06667	15.52333		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	354.6519	1	354.6519	54.00242	0.000732	6.607891
Within Groups	32.83667	5	6.567333			

Total	387.4886	6				

Table 6: ANOVA table for chlorophyll content in Getso plants at the end of irrigated and drought treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
irrigated	3	201.7	50.425	7.889167		
drought	4	129.6	43.2	16.21		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	89.48679	1	89.48679	7.977427	0.036916	6.607891
Within Groups	56.0875	5	11.2175			
Total	145.5743	6				

Table 7: ANOVA table for chlorophyll content between TVSU89 and Mana plants at the end of the irrigation treatment:

SUMMARY				
Groups	*Count*	*Sum*	*Average*	*Variance*
TVSU89	3	164.5	54.83333	8.803333
Mana	4	193.8	48.45	0.596667
ANOVA				

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	69.8519	1	69.8519	18.00616	0.008143	6.607891
Within Groups	19.39667	5	3.879333			
Total	89.24857	6				

Table 8: ANOVA table for chlorophyll content between TVSU89 and Getso plants at the end of the irrigation treatment

Groups	*Count*	*Sum*	*Average*	*Variance*		
TVSU89	3	164.5	54.83333	8.803333		
Getso	4	201.7	50.425	7.889167		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	33.3144	1	33.3144	4.035745	0.100786	6.607891
Within Groups	41.27417	5	8.254833			
Total	74.58857	6				

Table 9: ANOVA table for anthocyanin content of TVSU89 plants at the end of drought and irrigated treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	3	36.2	12.06667	2.893333		
Drought	3	28.8	9.6	0.67		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	9.126667	1	9.126667	5.122544	0.086364	7.708647
Within Groups	7.126667	4	1.781667			
Total	16.25333	5				

Table 10: ANOVA table for anthocyanin content of Mana plants at the end of drought and irrigated treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	4	40	10	2.326667		
Drought	3	19.8	6.6	0.57		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*

Between Groups	19.81714	1	19.81714	12.20267	0.01741	6.607891
Within Groups	8.12	5	1.624			
Total	27.93714	6				

Table 11: ANOVA table for anthocyanin content of getso plants at the end of drought and irrigated treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
irrigated	4	40.8	10.2	1.246667		
drought	3	21.3	7.1	0.19		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	16.47429	1	16.47429	19.99307	0.006571	6.607891
Within Groups	4.12	5	0.824			
Total	20.59429	6				

Table 12: ANOVA table for leaf numbers in TVSU89 and Mana plants at the end of the drought treatment

Groups	*Count*	*Sum*	*Average*	*Variance*
TVSU89	3	309	103	1

Mana	3	210	70	4		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	1633.5	1	1633.5	653.4	0.000013	7.708647
Within Groups	10	4	2.5			
Total	1643.5	5				

Table 13: ANOVA table for leaf numbers in Mana plants at the end of the irrigated and drought treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	4	601	150.25	40.91667		
Drought	3	210	70	4		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	11040.11	1	11040.11	422.1838	0.000548	6.607891
Within Groups	130.75	5	26.15			
Total	11170.86	6				

Table 14: ANOVA table for leaf numbers in Getso plants at the end of the irrigated and drought treatments

Groups	Count	Sum	Average	Variance		
Irrigated	4	532	133	39.33333		
Drought	3	228	76	19		
ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	5569.714	1	5569.714	178.5165	0.004201	6.607891
Within Groups	156	5	31.2			
Total	5725.714	6				

Table 15: ANOVA table for leaf fresh weights for all landraces at the end of irrigated and drought treatments

Groups	Count	Sum	Average	Variance		
Irrigated	12	536.3	44.69167	172.5827		
Drought	11	86	7.818182	8.805636		
ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	7803.231	1	7803.231	82.49217	0.001012	4.324794

Within Groups	1986.466	21	94.5936
Total	9789.697	22	

Table 16: ANOVA table for shoot fresh weights for all landraces at the end of irrigated and drought treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	12	536.3	44.69167	172.5827		
Drought	11	86	7.818182	8.805636		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	7803.231	1	7803.231	82.49217	0.00001736	4.324794
Within Groups	1986.466	21	94.5936			
Total	9789.697	22				

Table 17: ANOVA table for leaf dry weights of TVSU89 and Mana plants at the end of drought treatment

Groups	*Count*	*Sum*	*Average*	*Variance*
TVSU89	3	9.8	3.266667	3.163333
mana	4	19.9	4.975	1.2625

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	5.002976	1	5.002976	2.473252	0.176606	6.607891
Within Groups	10.11417	5	2.022833			
Total	15.11714	6				

Table 18: ANOVA table for leaf dry weights of TVSU89 and Getso plants at the end of drought treatment

Groups	Count	Sum	Average	Variance
TVSU89	3	9.8	3.266667	3.163333
Getso	4	12.5	3.125	0.009167

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	0.034405	1	0.034405	0.027073	0.875752914	6.607891
Within Groups	6.354167	5	1.270833			

	6.38857		
Total	1	6	

Table 19: ANOVA table for root fresh weights of getso and mana plants at the end of the drought treatment

Groups	*Count*	*Sum*	*Average*	*Variance*		
getso	4	36.5	9.125	7.229167		
mana	3	15.6	5.2	1.57		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	26.40964	1	26.40964	5.318627	0.069233	6.607891
Within Groups	24.8275	5	4.9655			
Total	51.23714	6				

Table 20: ANOVA table for root fresh weights of getso and TVSU89 plants at the end of the drought treatment

Groups	*Count*	*Sum*	*Average*	*Variance*
getso	4	36.5	9.125	7.229167
TVSU89	3	13.8	4.6	3.43

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	35.10107	1	35.10107	6.147836	0.055876	6.607891
Within Groups	28.5475	5	5.7095			
Total	63.64857	6				

Table 21: ANOVA table for root fresh weight of TVSU89 plants at the end of drought and irrigated treatments

Groups	*Count*	*Sum*	*Average*	*Variance*
Irrigated	3	25.9	8.633333	19.37333
Drought	3	13.8	4.6	3.43

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	24.40167	1	24.40167	2.140184	0.217314	7.708647
Within Groups	45.60667	4	11.40167			
Total	70.00833	5				

Table 22: ANOVA table for root fresh weight of Mana plants at the end of drought and irrigated treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	3	76	25.33333	255.2133		
Drought	3	15.6	5.2	1.57		
ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	608.0267	1	608.0267	4.735718	0.095151	7.708647
Within Groups	513.5667	4	128.3917			
Total	1121.593	5				

Table 23: ANOVA table for root fresh weight of Getso plants at the end of drought and irrigated treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	3	75.2	25.06667	71.96333		
Drought	4	36.5	9.125	7.229167		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*

Between Groups	435.663	1	435.663	13.15295	0.015113	6.607891
Within Groups	165.6142	5	33.12283			
Total	601.2771	6				

Table 24: ANOVA table for root dry weight of TVSU89 plants at the end of drought and irrigated treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	3	3.2	1.066667	0.123333		
Drought	3	1.4	0.466667	0.093333		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.54	1	0.54	4.984615	0.08935	7.708647
Within Groups	0.433333	4	0.108333			
Total	0.973333	5				

Table 25: ANOVA table for root dry weight of Mana plants at the end of drought and irrigated treatments

Groups	Count	Sum	Average	Variance		
Irrigated	3	6.6	2.2	1.57		
Drought	4	3.2	0.8	0.46		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	3.36	1	3.36	3.716814	0.11179	6.607891
Within Groups	4.52	5	0.904			
Total	7.88	6				

Table 26: ANOVA table for root dry weight of Getso plants at the end of drought and irrigated treatments

Groups	Count	Sum	Average	Variance		
irrigated	3	7.7	2.566667	2.203333		
drought	4	3.2	0.8	0.006667		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*

Between Groups	5.350476	1	5.350476	6.04346	0.057345	6.607891
Within Groups	4.426667	5	0.885333			
Total	9.777143	6				

Table 27: ANOVA table for leaf area index of all landraces at the end of irrigated and drought treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
irrigated	12	14003.1	1166.925	54820.85		
drought	11	3590.9	326.4455	15185.66		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	4054155	1	4054155	112.7816	0.00669	4.324794
Within Groups	754885.9	21	35946.95			
Total	4809041	22				

Table 28: ANOVA table for leaf area index of all landraces at the end of the drought treatment

Groups	Count	Sum	Average	Variance		
TVSU89	3	918.3	306.1	22741.27		
mana	4	1578.1	394.525	23076.13		
Getso	4	1094.5	273.625	2068.202		
ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	30941.11	2	15470.56	1.023561	0.40197	4.45897
Within Groups	120915.5	8	15114.44			
Total	151856.6	10				

Table 29: ANOVA table for root length per volume of TVSU89 plants at the end of both treatments

Groups	Count	Sum	Average	Variance		
Irrigated	3	66931.59	22310.53	25372812		
Drought	3	58762.49	19587.5	9404821		
ANOVA						
Source of Variation	SS	df	MS	F	P-value	F crit
Between Groups	11122365	1	11122365	0.639627	0.468648	7.708647
Within Groups	69555267	4	17388817			
Total	80677632	5				

Table 30: ANOVA table for root length per volume of Mana plants at the end of both treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	4	240829.6	60207.4	2.96E+08		
Drought	3	78273.2	26091.07	53882141		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	2E+09	1	2E+09	10.0048	0.02501	6.607891
Within Groups	9.97E+08	5	1.99E+08			
Total	2.99E+09	6				

Table 31: ANOVA table for root length per volume of Getso plants at the end of both treatments

Groups	*Count*	*Sum*	*Average*	*Variance*		
Irrigated	4	188604.6	47151.14	1.22E+08		
Drought	3	79313.07	26437.69	1765069		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	7.36E+08	1	7.36E+08	9.92801	0.025354	6.607891
Within Groups	3.7E+08	5	74084266			

Total	1.11E+09	6

Table 32: ANOVA table for root surface area of TVSU89 plants at the end of both treatments

Groups	Count	Sum	Average	Variance		
Irrigated	3	950.2733	316.7578	11148.06		
Drought	3	917.5656	305.8552	4245.104		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	178.2989	1	178.2989	0.023166	0.886395	7.708647
Within Groups	30786.33	4	7696.583			
Total	30964.63	5				

Table 33: ANOVA table for root surface area of Mana plants at the end of both treatments

Groups	Count	Sum	Average	Variance		
Irrigated	4	4842.414	1210.603	204092		
Drought	3	1055.8	351.9333	16970.57		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	1263967	1	1263967	9.779741	0.026038	6.607891
Within Groups	646217.2	5	129243.4			
Total	1910185	6				

Table 34: ANOVA table for root surface area of Getso plants at the end of both treatments

Groups	Count	Sum	Average	Variance
Irrigated	3	3494.519	1164.84	393796.4

Drought	3	1358.237	452.7458	196.3619		
ANOVA						
Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	760616.5	1	760616.5	3.861068	0.120865	7.708647
Within Groups	787985.6	4	196996.4			
Total	1548602	5				

Landrace	Treatment	LAI	Leaf fresh weight (g)	Shoot fresh weight (g)	Root fresh weight (g)	Leaf dry weight (g)	Shoot dry weight (g)	Root dry weight (g)	Pod number
TVSU89	Control	852.5	22.4	12.4	4.3	8.9	8.2	0.7	42
	Control	1107.9	33.3	17.7	8.5	11.2	7.8	1.1	33
	Control	900.3	30.8	20.5		9.3	11.4		22
	Control	1265.2	43.4	15.7	13.1	12	8.6	1.4	40
Mana	Control	1556.4	57.4	32.4		19.7	15.1		0
	Control	1491.3	57.8	26.6	29.8	18.8	10.6	3.4	0
	Control	805.1	28.4	11.7	7.6	9.6	5.3	2.3	0
	Control	1140.3	48.4	15.7	38.6	16	7.3	0.9	0
Getso	Control	1330.9	47	26.4	30.6	15.8	14.8	2.2	1
	Control	1222.1	51.7	42.2	15.3	16.2	17.4	1.3	0
	Control	1138.5	52.2	27.5	29.3	14	11.1	4.2	0
	Control	1192.6	63.5	30.7		17.3	13.5		0
TVSU89	Drought	470.3	10.8	7.1	6.5	5.2	4	0.8	2
	Drought	173.8	3.1	2.7	4.5	1.7	1.7	0.2	1
	Drought	274.2	4.8	4.7	2.8	2.9	2.5	0.4	0
Mana	Drought	492.8	11.3	7.7	6.5	4.9	3	0.6	0
	Drought	551.5	11	6	4	6.5	3.7	0.5	0
	Drought	301.2	5.6	2.8	5.1	4.7	2.4	0.3	0
	Drought	232.6	4.5	2.1		3.8	2	1.8	0
Getso	Drought	341.6	8.5	5.7	12.9	3.2	2.4	0.8	0
	Drought	245.6	7.2	6.2	7.1	3.1	5.8	0.7	0
	Drought	254.2	8.5	3.8	9.2	3	2	0.8	0
	Drought	253.1	10.7	5	7.3	3.2	2.3	0.9	0

Table 35: post-harvest data

Table 36: field data

Week 1

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	42.5	199	9.1	12
	43.2	186	7.8	12
	43.8	199	9.3	14
	43.2	208	10.5	7
	42.8	204	11.8	9
	39.6	194.6	11.2	13
	45.3	191.2	8.3	14
Mana	42.1	179.1	7.3	11
	38.9	187.6	7.8	9
	41.5	176	8.4	10
	38.2	176.2	8.3	8
	40.1	180.3	7.8	10
	36.9	176.7	7.9	9
	35.9	177.1	7.6	7
	39.8	183	8.1	8
Getso	39.7	179.4	7.8	11.3
	38.4	187.4	7.9	9.7
	40.9	179.7	8.6	12.3
	38.2	178.2	8.5	11
	40	179.4	8.1	10.9
	36.1	184.4	8.6	9.8
	32.5	184.9	8.7	8.7
	38	185	8.2	10.5

Week 2

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	49.1	202	9.6	20
	43.3	214.3	8.3	21
	41.3	211	9.4	23
	42.7	206	10.4	21
	49.5	213.8	11.3	21
	52.7	210.4	11.4	24
	49	214.3	9.1	29
Mana	41.2	197.2	8.4	14
	40.1	192.4	9.2	16
	41.9	198.4	8.6	17
	40.2	205.4	8.3	12
	39.8	211.2	9.1	13
	42.2	186.4	8.1	16
	42.6	180.3	7.5	15
	41.2	199.4	8.1	13
Getso	39.2	195	8.7	16
	38.1	192.8	9.3	15
	40	199.7	9.4	17
	42.6	204.5	9.2	16
	39.9	210.2	8.9	15
	41.1	176.7	9.4	13
	43	177.1	9.7	15
	38.7	197.4	8.4	17

Week 3

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	46	198.2	11.1	23
	44.7	193.4	10.4	21
	41	195.6	9.8	20
	43.5	197.3	10.3	19
	46.7	196.1	10.4	26
	45.3	190.5	9.6	27
	42.3	187.4	10.5	21
Mana	41.2	183.2	8.6	15
	39.7	184.6	8.7	18
	37.6	188.9	9.2	16
	33.1	183.8	9.2	14
	40.3	186.4	8.3	13
	38.9	182.1	8.4	11
	37.8	187.6	9	14
	39.7	181.2	8.3	15
Getso	42	192.3	9.6	21
	43.3	191.4	9.7	18
	38.7	189.6	9.8	20
	42.9	192.6	9.3	17
	37.1	186.4	10.2	19
	37.8	184.5	10.1	18
	35.1	185.3	9.3	19
	34.7	190.6	8.8	20

Week 4

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	49.7	208.1	13.1	40
	53.6	202.4	12.2	36
	47.8	203.4	11.8	36
	50.2	198.7	12.3	39
	53.2	205.8	11.2	38
	46.9	210.6	11.6	40
	42.3	212.3	11.9	37
Mana	40.2	186.5	9.8	27
	44.8	185.9	10.4	26
	45.8	190.2	11.1	29
	41.2	188.1	8.5	23
	38.4	183.9	8.9	25
	41.1	185.2	8.5	26
	41.6	182.9	8.9	35
	44.6	180.3	9.1	21
Getso	42.2	193.4	11.1	36
	41.9	192.4	10.7	37
	41.4	189.4	12.1	33
	39.7	188.9	10.6	32
	41.7	190.4	10.4	34
	43.9	194.5	10.1	39
	40.3	195.2	10.4	29
	43.4	196.7	11	32

Week 5

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	49.5	249	11.8	40
	51.6	213.6	11.1	43
	52.4	205.4	12.2	42
	45.9	240.6	10.5	38
	44.2	254.2	10.3	39
	49.8	248	12.3	44
	42.9	254.8	11.1	45
Mana	42.6	203.6	10.5	35
	44.2	196.8	10.1	34
	39.8	189.4	11	36
	37.3	193.6	10.4	30
	43.1	195.6	9.6	32
	46.9	192.3	9.8	28
	44.7	189.7	10.4	29
	42.4	193.6	9.8	28
Getso	44.6	203.3	10.6	36
	38.9	201.7	10.1	36
	42.7	198.6	9.7	38
	40.5	205.8	10.8	34
	48.6	197.9	10.9	40
	50.2	204.2	9.7	31
	49.2	200.4	10.5	32
	39.8	198.5	10.9	29

Week 6

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	52.3	218	11.2	64
	55.1	211.1	10.9	67
	49.8	219.4	10.4	58
	51.2	220.2	10.6	57
	49.2	198.7	9.7	58
	47.4	219.6	11.3	63
	47.8	211	10.1	61
Mana	46.8	188.4	9.1	42
	46.7	189.6	8.5	37
	44.6	191.4	9.5	44
	43.1	188.7	9.4	41
	44.1	186.4	9.5	38
	39.8	186.2	9.6	40
	41.3	182.6	9.1	42
	47.2	184.9	9.7	45
Getso	47.4	195.3	9.8	49
	46.8	191.9	9.4	51
	46.9	193.2	9.3	54
	43.8	197.5	9.5	46
	43.1	191.6	9.2	42
	49.8	189.2	9.7	41
	50.1	198.1	9.9	47
	45.7	190.2	10	54

Week 7

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	51	192.7	12.7	66
	52.5	190.2	12.6	67
	51.9	188.6	11.8	68
	55.2	179.8	10.6	62
	49.8	203.4	9.9	64
	52.3	194.2	11.2	65
	50.4	193.7	11.7	64
Mana	48.8	146.4	9.3	54
	47.6	136.7	7.7	56
	48.2	139.9	8.6	47
	43.6	137.8	8.2	51
	53.4	137.5	9.3	49
	52.7	136.1	7.9	56
	50.2	135	8.6	49
	49.9	139.4	8.4	53
Getso	53.3	168.3	11.1	53
	50.1	176.4	9.6	58
	49.2	162.9	10.2	62
	53.1	160.3	8.7	60
	52.7	162.9	9.3	58
	55.6	171.4	9.4	59
	47.2	168.7	10.4	63
	54	166.7	10.5	60

Week 8

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	58.2	206	11	86
	54.3	198.7	10.4	84
	50.7	204.1	10.1	83
	59.5	202.3	10.2	88
	57	204.5	10.6	87
	58.1	206.7	9.7	81
	54.5	198.8	10.1	86
Mana	51.6	190.2	9.6	66
	49.5	189.3	9.1	67
	53	187.6	8.9	62
	46.7	185.4	9.9	64
	47.2	186.9	9	61
	42.3	190.1	8.6	60
	52.4	184.3	9.4	58
	54.1	182.9	9.1	66
Getso	50.8	197.8	9.9	73
	49.7	196.8	9.6	70
	52.6	194.3	9.5	68
	45.7	192.5	10.1	67
	53	197.6	9.4	75
	54.9	199.3	9.8	79
	56.2	196.2	10.2	76
	50.7	199.1	9.1	68

Week 9

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	59.1	230	9.4	102
	58.6	240.3	10.2	107
	57.2	238	9.8	97
Mana	53.1	173.2	9.7	76
	52.6	174.2	9.3	83
	50.3	168.7	9.9	82
	52.8	172.3	9.5	77
Getso	54	203.2	10.7	92
	52.3	200.9	10.3	94
	53.1	205.8	10.3	88
	57	204.7	11.1	92
DROUGHT	**Chlorophyll Content**	**Stomatal Conductance**	**Anthocyanin**	**Leaf No.**
TVSU89	56.3	118.2	11.4	89
	52.7	116.2	11	90
	56.3	117.7	11.2	85
Mana	51.4	106.6	10.8	75
	50.6	104.2	10.4	70
	51.6	108.5	10.3	74
Getso	52.6	98.2	11.1	76
	53.6	100.6	10.5	75
	53.7	97.3	10.8	73

Week 10

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	60.2	249.3	9.9	150
	58	247.8	9.2	146
	61.2	243.9	9.1	151
Mana	51.7	180.2	10.2	101
	52	178.6	9.5	99
	50.8	179.4	10.1	94
	52	181.1	9.8	98.2
Getso	56	236	10.7	121.3
	54.1	227.8	10.2	118.8
	51.4	230.4	10.1	122.4
	46.8	229.7	10.8	119.9
DROUGHT	**Chlorophyll Content**	**Stomatal Conductance**	**Anthocyanin**	**Leaf No.**
TVSU89	54.2	97.2	10.2	91
	53.5	95.7	10.4	88
	54	95.8	9.7	94
Mana	53.6	54.2	11.2	79
	51.9	46.5	10.5	80
	50.8	51.4	10.4	73
Getso	50.7	80	11.3	71
	49.4	78.4	11.4	69
	48.9	80.2	10.9	76

Week 11

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	61.3	210.6	14.5	166
	59.8	215.3	13.9	173
	58.9	216.3	13.6	167
Mana	49.2	153.1	10.6	116.3
	48.7	149.4	9.8	112.9
	47.6	150.2	10.2	114.7
	50.1	148.1	9.7	115.3
Getso	53.6	125.4	12.3	128
	54.3	123.4	11.8	127
	49.5	119.6	11.6	122
	54.8	120.4	11.5	135
DROUGHT	**Chlorophyll Content**	**Stomatal Conductance**	**Anthocyanin**	**Leaf No.**
TVSU89	53.9	19.2	14.2	119
	54	18.2	13.2	112
	53.2	17.8	12.5	118
Mana	51	26.3	11.1	72
	49.6	27.1	10.6	79
	53.3	22.8	11	69
Getso	44.5	22.8	10.4	71
	49.2	25.5	10.4	69
	50.1	22.9	11.3	65

Week 12

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	58.3	247.2	10.2	171
	57.2	232.5	10.7	173
	55.9	246.7	9.4	167
Mana	52.9	203	10.2	122
	51.8	200.6	9.2	117
	50.7	197.6	8.4	120
	49.8	199.3	8.2	127
Getso	51.2	164.5	10.7	140
	50.6	162.9	11.2	128
	49.1	168.4	10.4	124
	52.7	159.8	10.9	138
DROUGHT	**Chlorophyll Content**	**Stomatal Conductance**	**Anthocyanin**	**Leaf No.**
TVSU89	51.9	38.4	11.6	106
	50.2	36.1	10.8	110
	49.7	37.5	11.8	99
Mana	44.5	21.9	8.4	78
	41.8	25.1	10.2	72
	45.4	24.8	7.9	66
Getso	47.2	31.4	8.1	64
	43.1	33.8	8.7	68
	45	35.6	8.2	60

Week 13

CONTROL	Chlorophyll Content	Stomatal Conductance	Anthocyanin	Leaf No.
TVSU89	55.2	247.2	10.8	180
	51.7	237.8	11.4	174
	57.6	240.4	14	172
Mana	49.3	204	8.7	149
	48.9	199.3	12.2	153
	47.7	207.1	9.7	157
	47.9	202.2	9.4	142
Getso	54.3	189.1	11.4	134
	47.8	192.9	8.8	141
	50.5	197	9.9	126
	49.1	199.8	10.7	131
DROUGHT	**Chlorophyll Content**	**Stomatal Conductance**	**Anthocyanin**	**Leaf No.**
TVSU89	45.2	33.6	8.7	104
	43.7	30.2	9.8	102
	44	34.1	10.3	103
Mana	38.4	22.1	6.7	72
	33.1	19.3	7.3	68
	30.7	19.7	5.8	70
Getso	38.8	25.3	7.6	81
	44.1	22.7	6.8	74
	46.7	25.2	6.9	73

Table 37: root parameters data

Landrace	Treatment	Length (cm)	Surface area (cm2)	Average diameter (mm)	Length per volume (cm/m3)	Root Volume (cm3)	Tips	Forks
TVS	Control	4151.9	433.3	0.3	27679.4	3.598	14461	30622
TVS	Control	2653.3	227.4	0.3	17688.5	1.551	28625	24463
TVS	Control	3251.3	289.6	0.3	21563.7	2.87	23221	26581
Mana	Control	10356.8	1674.1	0.5	69045.1	21.533	20850	163387
Mana	Control	9614.3	1294.1	0.4	64095.4	13.86	12419	130655
Mana	Control	5240.1	590.0	0.4	34934.1	5.287	10878	55830
Mana	Control	10913.3	1284.3	0.4	72755.1	12.027	15877	144737
Getso	Control	5868.1	962.0	0.5	39120.9	12.549	9397	63825
Getso	Control	5563.7	613.1	0.4	37091.4	5.376	11021	47906
Getso	Control	7779.2	1034.0	0.4	51861.3	10.936	12213	92416
Getso	Control	9079.7	1847.5	0.6	60531.1	29.915	11587	152990
TVS	Drought	3350.4	378.0	0.4	22335.0	3.393	9294	22009
TVS	Drought	2991.8	251.2	0.4	16279.0	1.8	6663	12355
TVS	Drought	3022.3	288.4	0.3	20148.5	2.19	5613	18060
Mana	Drought	6232.4	452.6	0.4	34072.3	4.7	8256	44782
Mana	Drought	3782.7	204.8	0.3	24571.7	3.2	3783	52811
Mana	Drought	4419.3	398.4	0.4	19629.2	1.8	4611	27982
Getso	Drought	4009.6	465.6	0.4	26730.9	4.302	6851	32420
Getso	Drought	3748.1	437.8	0.4	24987.0	4.069	5258	29707
Getso	Drought	4139.3	454.8	0.3	27595.2	3.977	7438	26451