

**DROUGHT TOLERANCE AND WATER-USE OF SELECTED SOUTH AFRICAN  
LANDRACES OF TARO (*COLOCASIA ESCULENTA* L. SCHOTT) AND BAMBARA  
GROUNDNUT (*VIGNA SUBTERRANEA* L. VERDC)**

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## DECLARATION

I, Tafadzwanashe Mabhaudhi, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original work and has not been submitted for any degree or examination at any other university.
2. This thesis does not contain data, pictures, graphs or other information from other researchers, unless specifically acknowledged as being sourced from other persons.
3. This thesis does not contain other persons' writing, unless acknowledged as being sourced from other researchers. Where other written sources have been quoted, then their words have been re-written and the information attributed to them has been referenced.
4. This study was funded by the Water Research Commission of South Africa WRC K5/177/4 Water-Use of Drought Tolerant Crops. WRC Knowledge Review 2008-09.

Signed \_\_\_\_\_

T. Mabhaudhi

Signed \_\_\_\_\_

Prof AT Modi (Supervisor)

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- Lastly, to my wife, Chenge, for all your love and support.

## DEDICATION

This work is dedicated to God Almighty who has blessed my life with all the people I call dear and cherish.

*Singabahambayo thina kulomhlaba siya ekhaya ezulwini*

*Tofamba munzira yakaoma, tine musha, wekudenga.*

## GENERAL ABSTRACT

Issues surrounding water scarcity will become topical in future as global fresh water resources become more limited thus threaten crop production. Predicted climate change and increasing population growth will place more pressure on agriculture to produce more food using less water. As such, efforts have now shifted to identifying previously neglected underutilised species (NUS) as possible crops that could be used to bridge the food gap in future. Taro (*Colocasia esculenta* L. Schott) and bambara groundnut (*Vigna subterranea* L. Verdc) currently occupy low levels of utilisation in South Africa. Both crops are cultivated using landraces with no improved varieties available. Information describing their agronomy and water-use is limited and remains a bottleneck to their promotion. The aim of this study was to determine the drought tolerance and water-use of selected landraces of taro and bambara groundnut from KwaZulu-Natal, South Africa.

In order to meet the specific objectives for taro and bambara groundnut management, an approach involving conventional and modelling techniques was used.

Three taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) and Umbumbulu (UM)] were collected from the North Coast and midlands of KwaZulu-Natal, South Africa, in 2010. The UM landrace was classified as Eddoe type taro (*C. esculenta* var. *antiquorum*) characterised by a central corm and edible side cormels. The DL and KW landraces were classified as Dasheen (*C. esculenta* var. *esculenta*), characterised by a large edible main corm and smaller side cormels. A bambara groundnut landrace was collected from Jozini, KwaZulu-Natal, and characterised into three selections ('Red', 'Light-brown' and 'Brown') based on seed coat colour. Seed colour was hypothesised to have an effect on seed quality. Field and rainshelter experiments were conducted for both taro and bambara landraces at Roodeplaat in Pretoria and Ukulinga Research Farm in Pietermaritzburg, over two growing seasons (2010/11 and 2011/12).

The objective of the field trials for taro and bambara groundnut was to determine mechanisms associated with drought tolerance in taro and bambara groundnut landraces. Experiments were laid out in a split-plot design where irrigation [fully irrigated (FI) and

rainfed (RF)] was the main factor and landraces (3 landraces of either taro or bambara groundnut) were sub-factors. Treatments were arranged in a randomised complete block design (RCBD), replicated three times. Rainfed trials were established with irrigation to allow for maximum crop stand. Thereafter, irrigation was withdrawn. Whilst experimental designs and layouts for taro and bambara groundnut were similar, differences existed with regards to plot sizes and plant spacing. Trials were planted on a total land area of 500 m<sup>2</sup> and 144 m<sup>2</sup>, for taro and bambara groundnut, respectively. Plant spacing was 1 m x 1 m for taro and 0.3 m x 0.3 m for bambara groundnut. Irrigation scheduling in the FI treatment was based on ET<sub>o</sub> and K<sub>c</sub> and was applied using sprinkler irrigation system.

Separate rainshelter experiments were conducted for taro and bambara groundnut landraces at Roodeplaat, to evaluate growth, yield and water-use of taro and bambara groundnut landraces under a range of water regimes. The experimental design was similar for both crops, a RCBD with two treatment factors: irrigation level [30, 60 and 100% crop water requirement (ET<sub>a</sub>)] and landrace (3 landraces), replicated three times. Irrigation water was applied using drip irrigation system based on ET<sub>o</sub> and K<sub>c</sub>.

Data collection in field and rainshelter trials included time to emergence, plant height, leaf number, leaf area index (LAI), stomatal conductance and chlorophyll content index (CCI). For taro field trials, vegetative growth index (VGI) was also determined. Yield and yield components (harvest index, biomass, corm number and mass) as well as water-use efficiency (WUE) were determined at harvest.

Intercropping of taro and bambara groundnut was evaluated under dryland conditions using farmers' fields at Umbumbulu, KwaZulu-Natal, South Africa. The experimental design was a RCBD replicated three times. Intercrop combinations included taro and bambara groundnut sole crops, a 1:1 (one row taro to one row bambara groundnut) and 1:2 intercrop combinations. The taro UM landrace and 'Red' bambara groundnut landrace selection were used in the intercropping study.

Lastly, data collected from field and rainshelter experiments were used to develop crop parameters to calibrate and validate the FAO's AquaCrop model for taro and bambara groundnut landraces. The UM landrace was used for taro while the 'Red' landrace selection

was used for bambara groundnut. AquaCrop was calibrated using observed data from optimum (FI) experiments conducted during 2010/11. Model validation was done using observations from field and rainshelter experiments conducted during 2011/12 as well as independent data.

Results showed that all taro landraces were slow to emerge ( $\approx 49$  days after planting). Stomatal conductance declined under conditions of limited water availability (RF, 60% and 30% ETa). The UM landrace showed better stomatal regulation compared with KW and DL landraces under conditions of limited water availability. Plant growth (plant height, leaf number, LAI and CCI) of taro landraces was lower under conditions of limited water availability (RF, 60% and 30% ETa) relative to optimum conditions (FI and 100% ETa). The UM landrace showed moderate reductions in growth compared with the DL and KW landraces, suggesting greater adaptability to water limited conditions. The VGI showed a large reduction in growth under RF conditions and confirmed the UM landrace's adaptability to limited water availability. Limited water availability (RF, 60% and 30% ETa) resulted in lower biomass, HI, and final yield in taro landraces relative to optimum conditions (FI and 100% ETa). For all trials, the DL landrace failed to produce any yield. WUE of taro landraces was consistent for the three irrigation levels (30, 60 and 100% ETa); however, on average, the UM landrace was shown to have a higher WUE than the KW landrace.

Bambara groundnut landraces were slow to emerge (up to 35 days after planting). 'Red' and 'Brown' landrace selections emerged better than the 'Light-brown' landrace selection, confirming the effect of seed colour on early establishment performance. Plant growth (stomatal conductance, CCI, plant height, leaf number, LAI and biomass accumulation) was lower under conditions of limited water availability (RF, 60% and 30% ETa) relative to optimum conditions (FI and 100% ETa). The 'Red' landrace selection showed better adaptation to stress. Limited water availability resulted in early flowering and reduced flowering duration as well as early senescence and maturity of bambara groundnut landrace selections. The 'Red' landrace selection showed delayed leaf senescence under conditions of limited water availability. Yield reductions of up to 50% were observed under water limited conditions (RF, 60% and 30% ETa) relative to optimum conditions (FI and 100% ETa). Water use efficiency increased at 60% and 30% ETa, respectively, relative to 100% ETa, implying

adaptability to limited water availability. The ‘Red’ landrace selection showed better yield stability and WUE compared with the ‘Brown’ and ‘Light-brown’ landrace selections suggesting that seed colour may be used as a selection criterion for drought tolerance in bambara groundnut landraces.

The intercropping study showed that intercropping, as an alternative cropping system, had more potential than monocropping. Evaluation of growth parameters showed that taro plant height was generally unaffected by intercropping but lower leaf number was observed as compared with the sole crop. Bambara groundnut plants were taller and had more leaves under intercropping relative to the sole crop. Although not statistically significant, yield was generally lower in the intercrops compared with the sole crops. Evaluation of intercrop productivity using the land equivalent ratio (LER) showed that intercropping taro and bambara groundnut at a ratio of 1:1 was more productive (LER = 1.53) than intercropping at a ratio of 1:2 (LER = 1.23).

The FAO’s AquaCrop model was then calibrated for the taro UM landrace and ‘Red’ bambara groundnut landrace selection. This was based on observations from previous experiments that suggested them to be drought tolerant and stable. Calibration results for taro and bambara groundnut landraces showed an excellent fit between predicted and observed parameters for canopy cover (CC), biomass and yield. Model validation for bambara groundnut showed good model performance under field (FI and RF) conditions. Model performance was satisfactory for rainshelters. Validation results for taro showed good model performance under all conditions (field and rainshelters), although the model over-estimated CC for the declining stage of canopy growth under RF conditions. Model verification using independent data for taro showed equally good model performance.

In conclusion, the taro UM landrace and ‘Red’ bambara groundnut landrace selection were shown to be drought tolerant and adapted to low levels of water-use. The mechanisms responsible for drought tolerance in the taro UM landrace and ‘Red’ bambara groundnut landrace selection were described as drought avoidance and escape. The taro UM landrace and ‘Red’ bambara groundnut landraces avoided stress through stomatal regulation, energy dissipation (loss of chlorophyll) as well as reducing canopy size (plant height, leaf number and LAI), which translates to minimised transpirational water losses. This indicated landrace



adaptability to low levels of water–use. The ‘Red’ bambara groundnut landrace selection showed phenological plasticity and escaped drought by flowering early, delaying leaf senescence, and maturing early under conditions of limited water availability. Performance of the ‘Red’ landrace selection lends credence to the use of seed coat colour as a possible selection criterion for drought tolerance in bambara groundnut, and possibly for other landraces with variegated seed. The taro UM landrace escaped drought by maturing early under conditions of limited water availability. The FAO’s AquaCrop model was successfully calibrated and validated for taro UM and ‘Red’ bambara groundnut landraces. The calibration and validation of AquaCrop for taro is the first such attempt and represents progress in the modelling of neglected underutilised crops. The calibration and validation of AquaCrop for taro requires further fine-tuning while that for bambara groundnut still needs to be tested for more diverse landraces.

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## **LIST OF ABBREVIATIONS**

AFLP – Amplified Fragment Length Polymorphism,

ARC-ISCW - Agricultural Research Council – Institute for Soil, Climate and Weather

ARC-VOPI – Agricultural Research Council – Vegetable and Ornamental Plants Institute

CCI – Chlorophyll content index

DAP – Days after Planting

DNA – Deoxyribonucleic acid

DWAF – Department of Water Affairs

FAO – Food and Agriculture Organisation

IWMA – International Water Management Institute

KZN – KwaZulu-Natal

LAI – Leaf Area Index

RAPD – Random Amplified Polymorphic DNA

RSA – Republic of South Africa

SC – Stomatal Conductance

SSR – Simple Sequence Repeats

UKZN – University of KwaZulu-Natal

WAP – Weeks after Planting

WRC – Water Research Commission

# CHAPTER 1

## INTRODUCTION AND GENERAL REVIEW OF LITERATURE

### 1.1 Conceptualisation and study objectives

According to the United Nations (2009), the world population is expected to reach 7 billion in 2012 and 9.1 billion in 2050. Much of this growth is expected to come from the developing world. This will result in increased pressure on fresh water resources needed to produce more food. Already, South Africa is one of the 30 driest countries in the world (The Water Wheel, 2007), with an annual average rainfall of less than 500 mm, a significantly lower amount than the world annual average of 860 mm (DWAF, 2002). According to the Water Act (RSA, 1998), South Africa's water resources are scarce and limited in extent. As a result, the International Water Management Institute (IWMA) has categorised South Africa a water stressed country (IWMI, 1996). The fact that recent climate change forecasts have predicted an increased frequency and intensity in the occurrence of droughts (Hassan, 2006) only serves to make the situation dire. This is of great concern when viewed within the context of the impacts all this will have on agriculture, and the vulnerability of rural households and the urban poor, regarding food and nutrition security, because the incidence of crop failure will likely increase (Sisulu and Scaramella, 2012). The threat has resulted in renewed focus on identifying and improving new and already existing crops for drought tolerance (Mabhaudhi, 2009).

In light of the aforementioned, there has recently been interest in the possible use and introduction of underutilised, indigenous and traditional crops as possible drought tolerant crops (Mabhaudhi, 2009). Underutilised indigenous and traditional crops can be defined as crops that have either originated in South Africa or those that have become "indigenised" over many years (>100 years) of cultivation and natural and farmer selection within South Africa (Schippers, 2002, 2006). In addition, these are crops that have not been previously classified as major crops, have previously been under-researched and currently have a low level of use that is mainly confined to small-scale farming areas (Azam-Ali, 2010). Historically, such crops have played an important role in ensuring community and household food security; most

of them have provided healthy alternatives when the main crop failed or during the periods in-between subsequent harvests. Most of these crops are believed to be adapted to a range of ecological niches and may have tolerance to abiotic and biotic stresses, chiefly heat and water stress. This makes them important future crops for small-scale farmers on marginalised lands and an important germplasm source for future crop improvements.

However, the promotion of elite, exotic and high yielding crops has occurred at the expense of underutilised, indigenous and traditional crops, in that the latter have been generally ignored by plant breeders and agronomists. That there was little or no research done on them has led to a scenario which deservedly earned them the title of “underutilised crops”. Thus, there currently exist very little literature describing their performance and adaptations to environmental stresses. Promotion of underutilised crops, with a view to reinstating them as major sources of food in agriculture will depend, to a large extent, on availability of information about their growth and development.

Taro (*Colocasia esculenta*) and bambara groundnut (*Vigna subterranea* (L.) Verdc), locally known as *Amadumbe* and *Izindlubu* in the Zulu vernacular, respectively, are two crops that fall within the category of underutilised crops. Researchers still argue about the exact origins of taro; what is certain, however, is that its origins lie outside of South Africa. Bambara groundnut, on the other hand, has its origins in the regions between the Jos Plateau in Northern Nigeria and Garu in Cameroon (Pasquet *et al.*, 1999). Although both of them have their origins outside of South Africa, they have both become traditional crops due to their extensive domestication. Little information currently exists describing the agronomy and water-use of taro, with regards to whether or not it is a drought tolerant crop (Lebot, 2009). Such information is urgently required if the crop is to be promoted as a possible drought tolerant crop. Thus, there is a need to generate information that can be used for policy formulation in order to successfully promote and reinstate taro and Bambara groundnut within rural households and boost their food and nutrition security. In the absence of extensive, and sometimes costly, agronomic trials, the use of calibrated and validated crop models may assist to generate such information.

Crop modelling has been defined as the dynamic simulation of crop growth by numerical integration of constituent processes with the help of computers (Sinclair and Seligman, 1996).

Crop models have been successfully used to predict growth and yield of crops (Jones and Ritchie, 1990), both temporally and spatially (Hillel, 1977). Simulation results can be used to evaluate production options and to show future areas of research. It is important to note that crop models are not and cannot be a substitute for field experiments. However, when calibrated and validated with data from field experiments, they can help lower the overall costs of field experiments with regards to time and space.

The primary aim of the proposed study was to evaluate the drought tolerance of selected landraces of Bambara groundnut and taro to water stress. Secondary to this, was to calibrate and validate FAO's AquaCrop model for taro and to create scenarios to answer questions with regard to growth and yield under conditions of water stress. Lastly, and to a limited extent, taro and bambara groundnut were compared for growth under conditions of intercropping in response to selected soil water regimes.

It is hypothesized that local landraces of taro and bambara groundnut may have acquired tolerance to drought stress through years of natural and farmer selection often under harsh conditions. It is further hypothesized that in bambara groundnut such drought tolerance may be linked to seed coat colour. Hence, the specific objectives of this study were:

- To understand the mechanisms of drought tolerance in taro and bambara groundnut with regards to growth, development and yield,
- To evaluate the growth, physiological and yield responses of taro and bambara groundnut to water stress,
- To calibrate and validate AquaCrop for taro and bambara groundnut,
- To evaluate the performance of the model with regard to its accuracy in predicting crop growth and water use of taro for different soils and weather conditions in South Africa, and
- To evaluate the feasibility of a taro-bambara groundnut intercrop under dryland conditions.



## 1.2 Underutilised indigenous and traditional crops

Currently between 300 000 to 500 000 plant species exist, out of which 30 000 are thought to be edible (Garn and Leonard, 1989). Throughout history, of the 30 000 edible plants, only 7 000 have been either cultivated or collected as food. Even more shocking is the fact that only 20 species have provided for 90% of the world's food requirements (Collins and Hawtin, 1999), with wheat, maize and rice accounting for 60% of man's diet (Collins and Hawtin, 1999). Thus, tens of thousands of edible plant species remain relatively "underutilised", with respect to their ability to contribute to the world's increasing food requirements. Consequently, there has been a reduction in genetic diversity underpinning agriculture; this is accompanied by the displacement of indigenous species by more favoured major crops (Azam-Ali, 2010). However, as Prescott-Allen and Prescott-Allen (1990) highlighted, the importance of many indigenous species should not be neglected.

The reduction in genetic diversity caused by focus on few staple crops has resulted in the occurrence of neglected underutilised species (NUS). However, unlike most staple crops, NUS are often well-adapted to local growing conditions (Padulosi, 1998), which are often marginal and harsh, thus offering sustainable food production (Idowu, 2009). Within the context of this study, NUS consist of crops that are indigenous or have been indigenised in South Africa. Based on the definitions forwarded by Schippers (2002, 2006), indigenous crops are those that have originated in South Africa while indigenised species are those that originated outside of South Africa, but have become domesticated over hundreds of years of on-farm cultivation and selection. Neglected underutilised species that are indigenous to South Africa include many *Amaranthus spp* (Laker, 2007), wild mustard and other wild edible leafy vegetables (Modi et al., 2006) while indigenised NUS comprise sweet potatoes (*Ipomoea batatas*), wild melon (*Curcubita spp*), taro and bambara groundnut. Historically, these crops have provided dietary support to the local communities. However, the promotion of the "major" crops, even in less suitable areas at times, has relegated NUS to their current status.

As already established (section 1.1), South Africa is a water-scarce country; more than 80% of the country is classified as hyper-arid to semi-arid (Bennie and Hensley, 2001). Water availability is a major limiting factor to crop production. As a result, this threatens the food security of vulnerable groups. Although previous studies have classified South Africa as being

food secure (De Klerk *et al.*, 2004), there is consensus that a large proportion of South Africans are vulnerable to household food insecurity and malnutrition (Steyn *et al.*, 2001; Rose and Charlton, 2002; De Klerk *et al.*, 2004). In addition, there is concern that most of the major crops are not adapted for cultivation under water stressed conditions (Baye *et al.*, 2001).

Neglected underutilized crop species are often described as “drought tolerant” (Zeven, 1998) and could therefore prove vital in fighting hunger. However, limited information describing basic aspects of their genetic potential, agronomy, water requirements and nutrition remains a hindrance to their development and promotion. Such information may be available in “grey literature” and/or indigenous knowledge systems, both of which are not peer reviewed. Therefore, the focus of this study was to develop scientific knowledge describing the genetic potential, agronomy and water requirements of two selected NUS in South Africa, taro and bambara groundnut.

## **1.3 Taro**

### ***1.3.1 Origins and history***

The origins of taro (*C. esculenta*) are still a point of debate, although its history in several centres of origin is well documented. According to Lebot (2009), the origins of taro have been studied by many researchers (Yen and Wheeler, 1968; Plucknett, 1984; Matthews, 1990; Lebot and Aradhya, 1991; Lebot, 1999). All the researchers concerned seem to have concurred that there is no single point of origin of taro. The main centre of origin is thought to be tropical Asia (Lebot, 2009), although several species could have originated elsewhere. What is certain is that taro is perhaps one of the oldest (if not the oldest) crops known to man. Suggestions of how long taro has been on earth range between 9,000 (Rao *et al.*, 2010) to 10,000 BC (Lebot, 2009). Lebot (2009) further advanced a hypothesis put forward by other authors (Cable, 1984; Plucknett, 1984; Haudricourt and Hédin, 1987) that rice may have been first discovered as a weed in taro fields!

The domestication of taro may have occurred several times in different locations ranging from India to South China, Melanesia and northern Australia (Lebot, 2009). The spread of taro from these centres into Africa may have been through the Mediterranean (Purseglove, 1979;

Leon, 1977; Plucknett, 1984), reaching Egypt about 2000 BP (Plucknett *et al.*, 1970). From there, it may have spread to the rest of Africa through trade and migration. In South Africa, taro is a traditional “indigenised” crop. Its Zulu name is *amadumbe* derived from the fact that it is most common in coastal areas and the hinterland of KwaZulu-Natal province (Modi, 2004). In addition, *amadumbe* is an important staple crop in the sub-tropical coastal areas starting at Bizana district in the Eastern Cape and the rest of coastal KwaZulu-Natal. The crop is also cultivated, to a lesser extent, in the sub-tropical and tropical regions of Mpumalanga and Limpopo provinces (Shange, 2004).

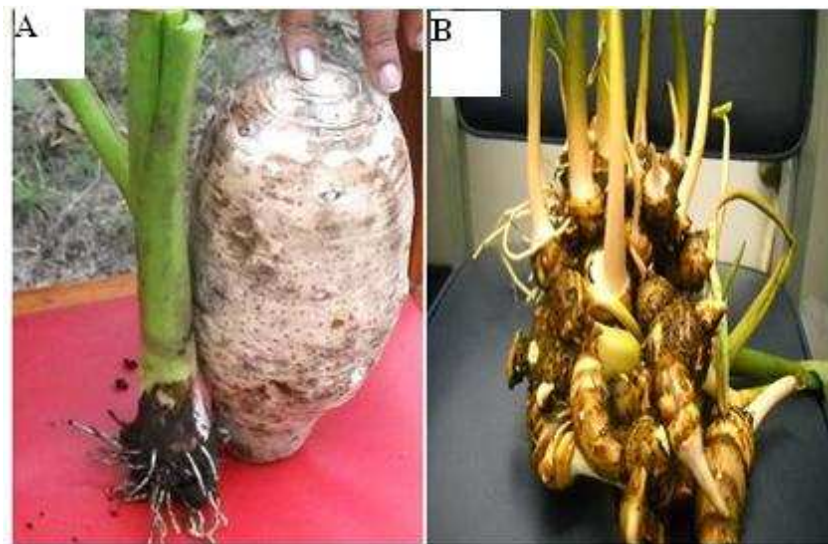
### **1.3.2 Botany and ecology**

Taro [*Colocasia esculenta* (L.) Schott] belongs to the family *Araceae*, sub-family *Aroideae*, whose members are more commonly referred to as aroids (Lebot, 2009). The family comprises about 110 genera with over 2,500 species divided amongst seven sub-families: *Acoroideae*, *Calloideae*, *Lasioideae*, *Monsteroideae*, *Pothoideae*, *Pistioideae* and *Aroideae* (Mayo *et al.*, 1997; Bown, 2000). Members of the aroid sub-family are found in almost every climatic region, with the exception of deserts and Polar Regions. Mare (2006) characterised local taro landraces in KwaZulu-Natal as belonging to the genus *Colocasia* and species *esculenta*. Members of the genus *Colocasia* are known to be monoecious and belong to the sub-family *Aroideae* (Lebot, 2009). Taro is one of the few edible species in the genus *Colocasia* (Ezumah, 1972) and is the most widely cultivated species (Vinning, 2003).

Some authors consider *C. esculenta* to be an allogamous and polymorphic species (Purseglove, 1979; Ivancic *et al.*, 2003) with two botanical varieties: *C. esculenta* var. *esculenta* (also called dasheen), and *C. esculenta* var. *antiquorum* (also called eddoe).

According to Lebot (2009), the main distinguishing factor between the two varieties lies in the shape and size of their main corms and cormels. Variety *esculenta* genotypes produce a large main corm and few, small side cormels – the edible part of which is the large central corm. The varieties in *antiquorum* genotypes are characterised by a relatively smaller central corm (compared with the dasheen) and numerous well-developed side cormels (Purseglove, 1972; Lebot and Aradhya, 1991; Lebot 2009); in South Africa, the side cormels are mostly

consumed while the central corm is usually kept for seed. Details of taxonomic and morphological differences between the two varieties have been described by Lebot (2009). The landraces that were considered for this study consist of both dasheen and eddoe varieties (Fig 1).



**Figure 1:** Two taro landrace varieties from KwaZulu-Natal: A) Var. *esculenta* – dasheen with one main corm and a *huli* used as planting material and, B) Var. *antiquorum* – eddoe with numerous side corms.

### ***1.3.3 Importance of taro***

Globally, taro is ranked fourteenth among staple vegetable crops with about 12 million tonnes being produced from about 2 million hectares of land (Rao *et al.*, 2010). The average yield estimate is 6.5 t/ha (FAOSTAT, 2012). The bulk of taro production is in Africa (Onwueme, 1999). In South Africa, taro is generally consumed as a subsistence crop (Shange, 2004), although some commercialisation has recently occurred. Farmers in Umbumbulu rural district of KwaZulu-Natal have come together and managed to market the crop to Woolworths and Pick ‘n Pay, which represent large retail outlets (Modi, 2003). This has elevated the production of taro and possibly resulted in more land being allocated to taro production in

KZN. The case of the Umbumbulu farmers is perhaps the only one where NUS have been successfully commercialised in South Africa. However, production still remains low and supply is challenged by obstacles in extending shelf life of taro (Mare, 2010). With improved information availability, taro production may be expanded together with commercialisation.

## **1.4 Bambara groundnut**

### ***1.3.1 Origins and history***

Bambara groundnut (*Vigna subterranea*), also known as *Nyimo* in Zimbabwe and *Jugo* beans or *Izindlubu* in South Africa, originated in North Africa and migrated with indigenous people to South Africa. Its name originates from Bambara, a district on the upper Niger near Timbuctoo. Bambara groundnut has been grown for centuries and has in the past contributed to the food security of Africa's poorest people (Swanevelde, 1998; FAO, 2001; Azam-Ali *et al.*, 2001; Mwale *et al.*, 2007a). However, due to the expansion of groundnut (*Arachis hypogea*) production, Bambara groundnut has been relegated to the status of an underutilized crop in most parts of Africa (Swanevelde, 1998).

Traditionally, it was cultivated in extreme, tropical environments by small-scale farmers without access to irrigation and/or fertilizers and with little guidance on improved practices. It is mainly grown by women for the sustenance of their families (Mukurumbira, 1985). Its protein content (16–25%) is comparable, and in some instances, superior to other established legumes, making it a good complement for cereal-based diets (Linnemann and Azam-Ali, 1993; Mwale *et al.*, 2007a). As an underutilized crop, its germplasm improvement and management practices have mainly relied on local experience and resources (indigenous knowledge) (Mukurumbira, 1985).

### ***1.4.2 Botany***

Bambara groundnut has been described as an annual legume with a strong well-developed tap root and a short lateral stem on which the leaves are borne. Growth of Bambara groundnut can be divided into distinct vegetative and reproductive phases. The vegetative stage involves

emergence and continuous production of leaves and elongation of roots. The leaves are trifoliate ( $\pm$  5 cm long) with the petiole approximately 15 cm long. Leaves are stiff and grooved, and the base is green or purple in colour. The flowers are typically papilionaceous and borne in a raceme on long, hairy peduncles which arise from the nodes on the stem. The reproductive phase begins at flowering. Bambara has two types of flowers/pollination, the first is usually self-pollinated, while the second is cross-pollinated by ants.. After fertilisation the flower stem elongates while the sepal enlarges and the fruit develops above or just below the soil surface. Pod colour varies according to ripeness from light yellow to black, purple and other shades. The seeds are round with a diameter of about 1.5 cm and are smooth and when dried, very hard. Seeds also vary in colour with cream, brown, red, mottled and white being the dominant seed colour (Swanevelder, 1998). In this study, seed colour was used as a criterion for selecting Bambara groundnut for water stress tolerance.

#### ***1.4.3 Bambara groundnut importance***

Bambara groundnut is grown in the semi-arid tropics where water is usually in short supply (Mwale *et al.*, 2007a). According to Linnemann and Azam-Ali (1993), within these communities, Bambara groundnut plays an important role as a protein source. In addition to being a source of dietary protein, the crop also replenishes nitrogen in the soil through nitrogen fixation. The ability of the crop to fix atmospheric nitrogen is important for resource-poor farmers who may otherwise not be able to afford inorganic fertilizers.

### **1.5 Drought and water scarcity**

Drought, within the context of crop production, is when there is insufficient water in the soil to support plant growth and development. This can occur as a result of a meteorological drought, poor rainfall distribution during the growing season and poor cultural practices which effectively reduce soil water content resulting in the plant being water stressed (Mabhaudhi, 2009). It has already been established in the preceding sections that South Africa is a water scarce country (The Water Wheel, 2007; DWAF, 2002; Water Act RSA, 1998; IWMI, 1996).

Water scarcity is mainly caused by a limited amount of water resources combined with low and uneven annual or seasonal rainfall.

Water is critical to crop production and food security (Wenhold *et al.*, 2007). Neglected underutilized species have been reported to have possibly evolved to tolerate harsh environments, including drought stress. However, more research still needs to be done to define and describe their responses to water stress as well as the mechanisms thereof.

## **1.6 Crop responses to water stress**

Plant or crop responses to water/drought stress vary and are dependent on the intensity and duration of the stress (Chaves *et al.*, 2002). Such responses are often described as being complex (Blum, 2011) and research is yet to fully elucidate all of them. An understanding of crop responses to water stress is important and fundamental to selection and breeding of drought tolerant crops. This is especially true in the case of NUS where there is a dearth of such information. The major crop responses to water stress are discussed below.

### ***1.6.1 Stomatal conductance***

Jaleel *et al.* (2009) defined drought stress as the moderate loss of water which results in stomatal closure and limitation of gas exchange. Stomatal conductance, measured by water flow, is the rate of diffusion of carbon dioxide (CO<sub>2</sub>) in and water molecules out of the leaf, which by extension represents opening and closure of stomata. It has previously been stated that closure of stomata (reduced stomatal conductance) is the first response of almost all plants to water stress (Mansfield and Atkinson, 1990; Cornic and Massacci, 1996). However, others have showed that cell expansion is more sensitive to water stress (Hsiao, 1973) suggesting that leaf growth may be the first. However, since stomatal closure is signalled for from the roots in response to depleting soil water, it stands to reason that stomatal closure is the first and foremost response to water stress. Plant stomata close in order to reduce transpirational water losses. Chaves *et al.* (2002) give a detailed description of stomatal closure in water stressed plants. Closure of stomata in response to stress has been associated with ABA signalling from drying roots (Gowing *et al.*, 1990; Davies and Zang, 1991). Field trials on several crops such

as maize (Tardieu *et al.*, 1991), grapevine (Correira *et al.*, 1995; Stoll *et al.*, 2000) and clover (Socias *et al.*, 1997) concurred with this hypothesis. In this study, stomatal closure was viewed as a crop response to decreasing soil water content.

Closure of stomata decreases the flow of CO<sub>2</sub> into the leaves, followed by a parallel decline in net photosynthesis, and ultimately plant growth. There is however ongoing debate as to whether drought mainly limits photosynthesis due to closure of stomata or metabolic impairment (Sharkey, 1990; Tezara *et al.*, 1999; Anjum *et al.*, 2003; Lawson *et al.*, 2003). However, general consensus has been that stomatal closure is the main reason for decreased photosynthesis under mild to moderate water stress (Cornic and Massacci, 1996; Chaves *et al.*, 2002, 2003; Yokota *et al.*, 2002). Collinson *et al.* (1997) ascribed drought resistance in bambara groundnut, in part, to effective stomatal control. Sivan (1995) studied drought tolerance in two taro varieties of dasheen and eddoe types, as well as tannia (*Xanthosoma sagittifolium*) and observed that stomatal conductance was lower under water stress relative to the well-watered conditions.

### ***1.6.2 Chlorophyll content***

Limitations to crop production caused by water stress are mostly due to limitations caused by water stress on photosynthesis. The capture of solar radiation, used in photosynthesis, and production of reducing powers is the preserve of photosynthetic pigments – mainly the chlorophyll a and b. Farooq *et al.* (2009) showed that these pigments are sensitive to water stress. In separate experiments conducted on barley (Anjum *et al.*, 2003) and by Farooq *et al.* (2009), water stress was shown to induce changes in the ratios and quantities of chlorophyll a and b as well as carotenoids. Chlorophyll content was shown to decrease in sunflower plants subjected to water stress (Kiani *et al.*, 2008).

Assessing alterations in pigment composition and content has now become an effective means of evaluating plant responses to stresses (Chen *et al.*, 2007). In separate reports by Estill *et al.* (1991) and Ashraf *et al.* (1994), chlorophyll b increased in two lines of okra, while chlorophyll a was unaffected; the overall effect was a reduction in the chlorophyll a:b ratio in both okra lines in response to water stress. Mensha *et al.* (2006) reported decreased



chlorophyll content in sesame subjected to water stress. In India, Sahoo *et al.* (2006) observed decreased chlorophyll stability index in a taro hybrid subjected to water stress using polyethylene glycol (PEG). Recently, Vurayai *et al.* (2011b), working on pot trials, reported that water stress did not have a significant effect on chlorophyll content index (CCI) of bambara groundnut landraces; they concluded that CCI was not reduced by water stress at all stages of growth. However, they recommended that their observations be evaluated further under field conditions.

### ***1.6.3 Plant growth and development***

Plant growth includes stages from germination, emergence up to and including vegetative growth. Plant growth is achieved through cell division (mitosis), expansion and finally differentiation. The processes of cell growth are some of the most sensitive ones to water stress due to reduction in turgor pressure (Taiz and Zeiger, 2006). In short, cell growth and consequently plant growth, is a turgor driven process. Thus, under water stress, turgor pressure is low, resulting in reduced cell division, expansion and differentiation; the observed effect of which is reduced plant growth.

According to Harris *et al.* (2002), the first and foremost effect of water stress is reduced germination and emergence. Kaya *et al.* (2006) stated that drought stress severely reduced germination and seedling stand. Water stress has been reported to reduce seedling establishment in several NUS – maize landraces (Mabhaudhi and Modi, 2010, 2011); wild mustard (Mbatha and Modi, 2010); wild melon (Zulu and Modi, 2010). Poor seedling establishment, as a result of water stress, leads to low yield due to reduced stand, and in most cases no amount of effort and/or expense later in the crop development can compensate for this deleterious effect (Mabhaudhi and Modi, 2010).

Water stress impairs mitosis, elongation and expansion, resulting in reduced plant height, leaf number and area and generally reduced crop growth (Nonami, 1998; Kaya *et al.*, 2006; Hussain *et al.*, 2008). Water stress has previously been reported to reduce plant height in potato (Heuer and Nadler, 1995) and soybean (Specht *et al.*, 2001; Zhang *et al.*, 2004. Bhatt and Rao (2005) associated the reduction in plant height with a reduction in cell expansion.

Leaf development is crucial to photosynthesis and dry matter production. Similar to plant height, water stress has been reported to affect leaf number and area in many crops, including soybean (Zhang *et al.*, 2004), cowpea (Manivannan *et al.*, 2007a), wheat and maize (Sacks *et al.*, 1997) and sunflower (Manivannan *et al.*, 2007b).

With regards to NUS, water stress was also shown to reduce plant height, leaf number and area in maize landraces (Mabhaudhi and Modi, 2010, 2011); wild mustard (Mbatha and Modi, 2010); wild melon (Zulu and Modi, 2010). Elsewhere, Sahoo *et al.* (2006) subjected a taro hybrid to water stress using PEG. They observed significant differences in plant growth parameters of height, leaf number and area in response to induced water stress. Furthermore, growth responses of bambara groundnut landraces to water stress have been previously studied (Collinson *et al.*, 1996, 1997; Mwale *et al.*, 2007b; Sinefu, 2011; Vurayai *et al.*, 2011a). They all reported reduced plant growth (plant height, leaf number, leaf area, leaf area index) in response to water stress. However, work on bambara groundnut still requires more research since all research has been done on landraces and landraces have a lot of a variation within and amongst themselves. This implies that the results cannot be easily transferred to other landraces. In a study on drought tolerance of dasheen and eddoe taro cultivars by Sivan (1995), water stress was shown to reduce leaf number, and leaf area of both cultivars; the greatest decrease in leaf area was in the eddoe type cultivar. Reduction in leaf number and area was attributed to premature senescence of old leaves.

In principle, the root is the only plant part responsible for sourcing water which is used by the plant. Therefore, the importance of the root system with regards to a plant's ability to tolerate stress has been well established (Jaleel *et al.*, 2009). Hypothetically, under water stress, the root will grow until a plant's demand for water is met; however, genetic variations may limit potential maximum rooting depth (Blum, 2005). Several studies have reported increased root growth in plants subjected to water stress – sunflower (Tahir *et al.*, 2002), *Phoenix dactylifera* (Djibril *et al.*, 2005) and *Populus sp* (Wullschleger *et al.*, 2005). Increased root growth under stress has been associated with an increased root:shoot ratio; under stress, plants will allocate more assimilate to root growth (sourcing more water) while limiting stem and leaf growth (loss of water).

Increased root:shoot ratio of dry matter has been reported in bambara groundnut (Collinson *et al.*, 1996; Vurayai *et al.*, 2011a) under water stressed conditions. Sivan (1995) also reported increased root:shoot ratio, on a dry matter basis, in dasheen and eddoe cultivars of taro; the eddoe cultivar was shown to increase root:shoot ratio in response to both moderate and severe water stress. However, Blum (2005) argued that the increase in root:shoot dry matter ratio in response to stress may not necessarily be due to increased dry matter partitioning to the roots, but rather reduced partitioning to the leaf as well as leaf senescence. Blum (2005) further argued that root length may increase under stress at a reduced total root mass. However, despite differences in perception, a well-developed root system allows for enhanced capture of soil water; an important drought adaptation response (Vurayai *et al.*, 2011a).

#### **1.6.4 Yield**

Yield refers to the harvestable portion of the crop. The objective of every farmer is to achieve high yields (Jaleel *et al.*, 2009) under all conditions, more so under drought stress. The objective of many breeding programmes is to develop a crop that will produce high yields under all environmental conditions (Blum, 2005), including drought. However, crop yields show considerable variation under drought stress conditions (Jaleel *et al.*, 2009).

According to Farooq *et al.* (2009), many yield-determining plant processes are affected by water stress. Farooq *et al.* (2009) provided a detailed table highlighting percentage yield reductions for a wide variety of crops in their review of effects of plant drought stress on crop growth. Water stress has been reported to reduce yields in cotton (Pettigrew, 2004), pearl millet (Yadav *et al.*, 2004), and in barley (Samarah, 2005). Studies have also shown yield reduction in response to water stress in legume crops such as soybeans (Frederick *et al.*, 2001) and black beans (Nielson and Nelson, 1998). The effect of water stress on yield of bambara groundnuts has also been studied; reports showed reduced yield in response to water stress (Mwale *et al.*, 2007a, b; Sinefu, 2011; Vurayai *et al.*, 2011a). Despite popular belief that taro is a water loving plant, Sahoo *et al.* (2006) reported negligible yield reduction in a taro hybrid subjected to PEG induced water stress. They concluded that the development of drought

tolerant taro cultivars was possible. Therefore, evaluating responses of previously unstudied taro landraces to water stress may aid in identifying genotypes with drought tolerance.

### ***1.6.5 Physiological responses to water stress***

In addition to morphological and phenological adaptations to water stress, the plant also employs several physiological mechanisms to help cope with stress. These include, but are not limited to, osmotic adjustment, osmoprotection, osmoregulation and antioxidant defence systems.

#### ***1.6.5.1 Compatible solutes***

Tolerance to water stress involves accumulation of several compatible organic solutes in the cytosol (Serraj and Sinclair, 2002) which act to protect plants from stress by assisting in osmotic adjustment, detoxification of reactive oxygen species (ROS), enhancing membrane stability as well as protein structure and integrity (Farooq *et al.*, 2009). Such metabolites include proline and soluble sugars.

Proline is a widespread plant response to water stress (Yancey *et al.*, 1982). Proline accumulation is due to increased biosynthesis and slower oxidation in mitochondria via the  $\Delta$ 1-pyrroline-5-carboxylate (P5C); a reaction catalysed by P5C reductase; P5Cs have been shown to increase in response to drought stress (Samaras *et al.*, 1995). Positive roles for proline have been suggested, including stabilisation of macromolecules, a sink for excess reductants, and a store of carbon and nitrogen for use following relief of water stress (Smirnoff and Stewart, 1985; Smirnoff and Cumbe, 1989; Samaras *et al.*, 1995). In certain plant species, proline plays a major role in osmotic adjustment (e.g. in potato), while in others, such as in tomato, proline accounts for only a small fraction of the total concentration of osmotically active solutes (Claussen, 2005). Verslues and Sharp (1999) suggested that proline had a clear role as an osmoticum due to high concentrations observed under stress. Garcia *et al.* (1987) reported that free proline levels significantly increased in maize seedlings in response to water stress; Mabhaudhi (2009) also observed proline accumulation in water stressed seedlings of maize landraces. de Ronde *et al.* (2000) detected that with decreasing soil water content, there was a progressive increase in free proline in six cotton cultivars. Proline

accumulation has a role in plant acclimation to water stress, depending on the plant and variety; it may therefore be used as an index for drought stress tolerance.

#### *1.6.5.2 Antioxidants*

On a whole plant level, exposure to water stress often results in reduced photosynthesis and growth as described in preceding sections. However, at the molecular level, a consequent of water stress is the plethora in ROS which cause oxidative damage. The ROS produced include superoxide anion radicals ( $O_2^-$ ), hydroxyl radicals ( $OH^-$ ), hydrogen peroxide ( $H_2O_2$ ), alkoxy radicals (RO) and singlet oxygen ( $O_2^1$ ) (Munné-Bosch and Pennuelas, 2003). Accumulation of ROS has been linked to an excess of energy due to stress-induced limitations on PSII (Demmig-Adams and Adams, 1996). Reactive oxygen species have been reported to cause oxidative damage by reacting with proteins, lipids and DNA; hence impairing normal cellular metabolism (Foyer and Fletcher, 2001). Plants have, however, evolved mechanisms to help alleviate oxidative stress by producing an array of enzymatic and non-enzymatic antioxidants like  $\alpha$ -tocopherol, superoxide dismutase, catalase, and enzymes of the ascorbic glutathione cycle (Foyer *et al.*, 1994). Catalase is the principal  $H_2O_2$  scavenging enzyme (Asada, 1999). Abdel-Kader (2001) observed increased catalase activity in response to water stress in two lettuce cultivars and concluded that catalase was associated with drought tolerance.

### **1.7 Mechanisms of drought tolerance**

A plant's chosen mechanism to coping with stress is based on the choice of responses it adopts in responding to developing water stress. Based on this combination, and the magnitude and timing of stress (Blum, 2005), a plant may escape, avoid, and/or tolerate stress.

#### *1.7.1 Drought escape*

Drought escape is mainly associated with occurrence of phenological stages. Plants that escape drought achieve this by having a short growing season, allowing them to complete their growth cycle before water stress becomes terminal. According to Araus *et al.* (2002), flowering is an important adaptation related to drought escape. They further stated that escape

occurs when crop phenology, such as time to flowering, is closely synchronised with periods of water availability, particularly when the growing season is characterised by terminal drought (Farooq *et al.*, 2009). The only negative to drought escape is that yield is generally correlated with length of crop duration as this translates into the period of active photosynthesis. Therefore, shortened growth duration will result in decreased yield as the period of active photosynthesis is reduced as well as the size of the photosynthetic factory.

### ***1.7.2 Drought avoidance***

The essence of drought avoidance is to reduce water loss while enhancing or maintaining uptake by the roots. Drought avoidance involves crop responses such as stomatal regulation, enhanced capture of soil water through an extensive and prolific root system (Turner *et al.*, 2001; Kavar *et al.*, 2007). Several root characteristics such as biomass, length, depth and thickness (volume) are thought to contribute towards final yield under drought stress (Subbarao *et al.*, 1995; Turner *et al.*, 2001; Kavar *et al.*, 2007) due to improved water capture. Additionally, morphological changes can help the plant to reduce water losses; reduced plant height, leaf number, leaf area and leaf area index (LAI) all contribute towards reducing water losses by the plant (Mitchell *et al.*, 1998) thereby assisting the plant to avoid drought. Blum (2004) also associated drought avoidance with reduced season duration due to reduced leaf number; reduced season duration is also characteristic of drought escape, suggesting that the mechanisms do not work in isolation. However, as with drought escape, the crop responses that are employed to avoid drought are at the expense of dry matter production and hence yield.

### ***1.7.3 Drought tolerance***

Drought tolerance has been defined as the plant's capacity to maintain metabolism under water stress (Blum, 2005). It includes osmotic adjustment (accumulation of metabolites, osmoprotection (e.g. proline) and the antioxidant defence systems (Farooq *et al.*, 2009). Blum (2005) gave a detailed account of increasing evidence suggesting a relationship between high osmotic adjustment and maintenance of biomass and yield under stress. Unlike escape and

avoidance, the *modus operandi* of drought tolerance does not show any solid evidence of a yield reduction (Blum, 2005). However, drought tolerance as an effective crop drought-resistance mechanism is rare; it mainly exists in seed embryo and is lost after germination (Blum, 2005). Nonetheless, it is an important crop mechanism for dealing with stress.

## **1.8 Crop modelling**

A crop model is a simplified representation of a real system (Hillel, 1977; de Wit, 1982). Sinclair and Seligman (1996) defined crop modelling as the dynamic simulation of crop growth by numerical integration of constituent processes with the aid of computers. Uses of crop models span from the farm level to regional levels. Models can assist as decision support tools for planning (Steduto *et al.*, 2009), decision making, yield forecasting, evaluating effects of climate change as well as for identifying research gaps. According to Singels *et al.* (2010), models are also useful in the integration of knowledge and data across disciplines; multidisciplinary research has recently been advocated as the way forward in terms of research. With regards to decision support, Steduto *et al.* (2009) suggested two classes of support – strategic (land-use, climate change, sustainability) and tactical (cultivar selection, fertilisation, plant populations etc) while Singels *et al.* (2010) added a third class – operational support (irrigation scheduling, weeding etc).

The variety of applications of crop models has made them an essential tool in agricultural systems. South Africa has also been part of the global advancement in modelling; over the years, South Africa has developed several of its own models – ACRU (Schulze, 1975), BEWAB and SWAMP (Bennie *et al.*, 1988, 1997, 1998), CANEGRO (Inman-Bamber, 1995; Inman-Bamber and Kiker, 1997) and CANESIM (Singels and Donaldson, 2000), PUTU (de Jager, 1974; Kaiser and de Jager, 1974), SAPWAT (Crosby and Crosby, 1999), and SWB (Annandale *et al.*, 1999). In addition, several other international models have been successfully used in South Africa. These include CERES and CROPGRO which are housed in DSSAT (IBSNAT, 1993; Jones *et al.*, 1998; Uehara and Tsuji, 1998) and APSIM (McCown *et al.*, 1996; Keating *et al.*, 2003). Singels *et al.* (2010), in their review of the history of crop modelling in South Africa over 25 years (1983-2008), reported that, given South Africa's limited manpower and resources, the scope of model development and application was

plausible. However, more still needs to be done in order to bring South Africa on par with global developments and trends. The recent involvement of South Africa in global projects such as the Agricultural Model Intercomparison and Improvement Project (AGMIP) (<http://www.agmip.org>) is a step in the right direction. Furthermore, such efforts should involve working on new local and international models, adapting them to South African conditions, and modelling underutilised and indigenous crops.

### ***1.8.1 Approaches to modelling***

Several authors (Bouman *et al.*, 1996; Passioura, 1996; Monteith, 1996; Boote *et al.*, 1996; Fischer *et al.*, 2000; Hammer *et al.*, 2002) have reviewed the different approaches to modelling, as well as their advantages and limitations. These included regression or empirical models, stochastic models, parameter models, and deterministic models. This review will focus on deterministic models.

Deterministic or mathematical models attempt to mimic, in as much as is feasibly possible within calculation time, the actual processes known to occur in the SPAC (Savage, 2001). They attempt to explicitly represent causality between variables (Whisler *et al.*, 1986) and their observed behaviour based on the physical laws controlling flow of mass and energy that can be described mathematically (Hillel, 1977; Savage, 1993; Savage, 2001). Hence their increased accuracy and precision. A distinction between deterministic models can be drawn between a mechanistic and functional approach (Hillel, 1977; Wagenet, 1988; Passioura, 1996; Savage 2001). For the purposes of this study, we shall focus more on both the mechanistic and functional approaches.

#### ***1.8.1.1 Mechanistic approach***

The mechanistic approach has also been described as a *scientific* approach to describing knowledge. Its aim is to improve our knowledge and understanding of the crop with regards to crop growth and development, physiology, and responses to environmental changes (Steduto *et al.*, 2009).



### *1.8.1.2 Functional approach*

This has also been described as an engineering approach to solving problems and is selected to fit observed field and laboratory measurements (Monteith, 1996). They attempt to provide sound management advice to farmers or predictions to policymakers (Passioura, 1996).

It must however be noted that the distinction between these two approaches is seldom as lucid. In practise, and to varying degrees of emphasis, most models may contain aspects of the two approaches and serve both purposes (Karunaratne, 2009; Singels *et al.*, 2010).

### *1.8.2 An overview of major crop models*

Azam-Ali *et al.* (1994) stated that at the core of any crop model, lies a set of equations designed to estimate production rate of biomass from captured resources such as carbon dioxide, solar radiation and water. Steduto (2003) categorised modelling biomass production into three approaches: carbon-driven, radiation-driven and water-driven models.

The so-called school of de Wit is credited for the carbon-driven biomass production approach (de Wit, 1965; de Wit *et al.*, 1970). These base crop growth on carbon assimilation by the leaf via photosynthesis (Todorovic *et al.*, 2009) and includes WOWorld FOod Studies (WOFOST; Van Diepen *et al.*, 1989; Boogard *et al.*, 1998) as well as other Wageningen crop models (Bouman *et al.*, 1996; Van Ittersum *et al.*, 2003) and the American CROP GROwth model (CROPGRO; Boote *et al.*, 1998, 2002). Van Ittersum *et al.* (2003) provide a detailed and particularly interesting review of the Wageningen models since de Wit (1958) to date.

Radiation-driven crop models rely on conversion of intercepted solar radiation to radiation use efficiency (RUE) as the basis for calculating biomass (Monteith, 1977). Intermediary steps such as leaf quantum efficiency per unit of CO<sub>2</sub> fixed, photo- and dark respiration rates, are thought to be incorporated into RUE (Monteith, 1977). This reduces their level of complexity and input requirements compared with carbon-driven modules. Models such as the Crop Environment Resources Synthesis (CERES; Ritchie *et al.*, 1985; Jones and Kiniry, 1986; Jones *et al.*, 2003), Erosion Productivity Impact Calculator (EPIC; Jones *et al.*, 1991), and Simulator mulTIdisciplinary for Crop Standard (STICS; Brisson *et al.*, 2003) (adapted from Todorovic *et al.*, 2009).

Water-driven crop models are based on an approach postulated by several authors from as early as 1958 (de Wit, 1958) to most recently (Hanks, 1983; Tanner and Sinclair, 1983; Hsiao and Bradford, 1983; Steduto, 1996; Steduto and Albrizio, 2005). Biomass accumulation is a function of transpiration and a water productivity (WP) parameter. Water-driven models are less complex with few input requirements (Steduto *et al.*, 2007, 2009). The main advantage of water-driven models compared to radiation-driven models, lies in the normalisation of the WP parameter for climate (both ETo and atmospheric CO<sub>2</sub>) thus giving them wider applicability in space and time (Steduto and Albrizio, 2005; Hsiao *et al.*, 2007; Steduto *et al.*, 2007). Notable models, which come to mind include CropSyst (Stockle *et al.*, 2003), which has both RUE and a vapour pressure deficit (VPD)-driven component and the FAO's model – AquaCrop (Steduto *et al.*, 2009; Raes *et al.*, 2009). CropSyst requires 40 parameters to run it while AquaCrop only requires 33 crop input parameters to run (Todorovic *et al.*, 2009).

The focus of this study is on describing drought tolerance of selected landraces of taro and bambara groundnut. Therefore, emphasis is on yield response to water such that a water-driven model would be most suited to this study. Although several water-driven models have been used to predict yield response to water, only AquaCrop has recently been used for underutilised crops. Therefore, within the context and scope of this study focus was restricted to the water-driven models with particular emphasis on AquaCrop.

### ***1.8.3 Introducing the FAO's AquaCrop model - concepts and underlying principles***

AquaCrop is a water-driven, canopy level, engineering (functional) type model whose primary focus is to simulate attainable crop biomass and yield in response to water (Steduto *et al.*, 2012). The model is an evolution of Doorenbos and Kassam's (1979) initiative, published in FAO's Irrigation and Drainage Paper No.33. At the core of their paper was the following equation:

$$\left(\frac{Yx-Ya}{Yx}\right) = Ky \left(\frac{ETx-ETa}{ETx}\right) \quad \text{Equation 1}$$

where Yx = maximum yield

$Y_a$  = actual yield

$ET_x$  = maximum evapotranspiration

$ET_a$  = actual evapotranspiration, and

$K_y$  = proportionality factor between relative yield loss and relative reduction in evapotranspiration.

The FAO's irrigation scheduling model CROPWAT (Smith, 1992) uses Eq. 1 to simulate yield under water deficit. In South Africa, SAPWAT (Crosby and Crosby, 1999) also uses this approach to calculate crop yields. The successes of both CROPWAT and SAPWAT, with regard to uptake by end-users, speak volumes about Eq. 1. In South Africa, SAPWAT has been fully adopted by the former Department of Water Affairs and Forestry (DWAFF) as a tool for determining irrigation water allocations in relation to licensing of agricultural water use (Singels *et al.*, 2010). However, as progress in understanding plant water relations would dictate, and also due to the need for increased water productivity as a result of increasing water scarcity, the FAO had to upgrade Eq. 1. A decision was taken to develop a new crop model as an evolution from Doorenbos and Kassam (1979). The new model would remain water-driven, as well as retain the broad spectrum applicability of Eq. 1, while also making ground breaking improvements in accuracy and still maintaining the hallmark of a robust and simple model. It is to this end that FAO has developed AquaCrop (Raes *et al.*, 2009; Steduto *et al.*, 2009; Steduto *et al.*, 2012).

According to Steduto *et al.* (2009) (Figure 2), the evolution lies in AquaCrop's capacity to:

- I. separate ET into crop transpiration ( $T_r$ ) and soil evaporation ( $E$ ). Previously, in Eq. 1 these were combined and this caused challenges with regards to the unproductive use of water lost through  $E$ , especially during crop establishment when ground cover is still very low,
- II. estimate  $T_r$  and  $E$  based on a simple canopy growth and decline model,

- III. treat final yield (Y) as a function of biomass (B) and harvest index (HI), thus allowing for the distinction of functional relations between the environment and B, and between the environment and HI,
- IV. segregate responses to water stress into four separate components –
  - a. canopy growth
  - b. canopy senescence
  - c. Tr, and
  - d. HI.

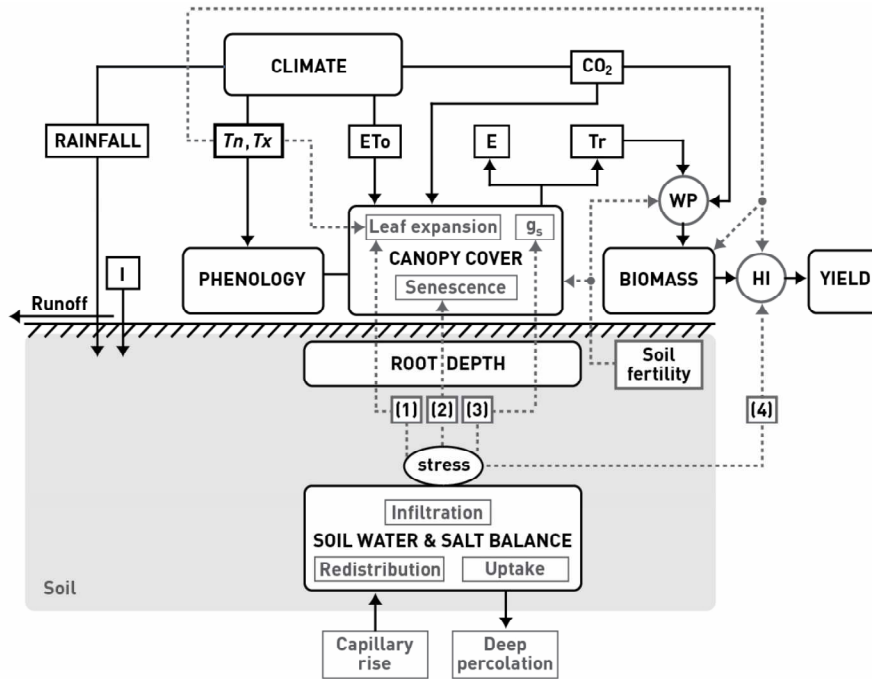
The above changes led to the equation at the core of AquaCrop:

$$\mathbf{B = WP \times \Sigma Tr} \qquad \mathbf{Equation 2}$$

Where, B = biomass,

WP = water productivity (biomass per unit of cumulative transpiration), and

Tr = crop transpiration.



**Figure 2:** Flowchart of AquaCrop indicating the structural relationships in the SPAC (adapted from Raes *et al.*, 2009).

Fundamental to Eq. 2 is the WP parameter which tends to be constant over different soils and climatic conditions as described by de Wit (1985), Hanks (1983) and Tanner and Sinclair (1983). In addition, normalization of WP for different climatic conditions further makes it a conservative parameter (Steduto *et al.*, 2007), implying greater applicability, robustness and transferability of the model between and among users in varying regions of the world. The other important improvement from Eq. 1 is that Eq. 2 can operate on a daily time step thus approaching the time scale of plant responses to water stresses (Acevedo *et al.*, 1971), while Eq. 1 operated on a seasonal time scale.

There are, however, similarities between AquaCrop and other established models with regards to structure of the SPAC. As with other models, AquaCrop includes the soil (soil water balance), the plant and the atmosphere as structural components of the model (Steduto *et al.*, 2009). The atmosphere and soil components bear similarities to other models. It is the relationship between the crop and soil components that distinguishes AquaCrop from other known models. Under its management component, there is particular emphasis on irrigation,

with soil fertility also being considered to a limited extent. AquaCrop, however, does not consider other biotic factors such as pests and diseases (Steduto *et al.*, 2009).

The review of modelling has shown that there has been much progress in the development and understanding of crop models. However, a lot of this progress and most of the models currently developed are for the major crops. There have been very limited efforts to develop models for NUS. Perhaps, it is in this regard that AquaCrop leads. Although the model is still in its infancy, it has already been calibrated and validated for some NUS – quinoa (Geerts *et al.*, 2009) and bambara groundnut (Karunaratne *et al.*, 2011). These efforts form stepping stones to modelling of other NUS. A huge gap currently exists in this regard. As such, part of the focus of this study was to also contribute to international efforts on modelling yield response to water availability of NUS through calibrating and validation AquaCrop for local landraces of taro and bambara groundnut.

### **1.9 Mitigating some effects of drought: Intercropping**

Predicted climate change (de Wit and Stankiewicz, 2006; Hassan, 2006) poses a significant threat to the hegemony held by major crops and sole cropping, as a practice (Baye *et al.*, 2001). This poses a serious threat to global food security, especially in the tropics. The need to identify “new” drought tolerant crops is also shared by the need to explore alternative farming practices such as intercropping. Although such efforts have taken off, albeit slowly, they appear to be occurring separately. Studies on intercropping have been focused on evaluating mostly cereal-legume intercrop combinations of the major crops. On the other hand, studies on NUS have primarily been conducted as sole crops. It is imperative that intercrops comprising NUS be also studied. In a future whereby water is set to become more limiting, intercropping NUS could hold the key to maximizing resource utilization.

Intercropping has been defined as the growing of two or more different crop species “simultaneously” on the same piece of land or field in both space and time and with overlap at least during part of each crop’s growing season (Willey, 1979; Ofori and Stern, 1987; Baldy and Stigter, 1997). Within the context of an intercrop, “simultaneous” implies that the crops grow together for a significant part of their growing periods. Other authors (Willey, 1979) have used this to distinguish intercropping from relay cropping, although the latter is generally

accepted as a form of intercropping. The spatial arrangements of the component crops can be arranged in several ways, which may include, but are not limited to:

- i. row intercropping – growing two or more crops at the same time with at least one crop planted in rows. This system is more aligned to conventional agriculture and will serve as the scenario for the case study described in this review,
- ii. strip intercropping – growing two or more crops together in strips wide enough to allow for separate, mechanized crop production. This arrangement is often most desirable whereby at least one or both crops are to be machine harvested; however, the component crops should remain in proximity to allow for interaction,
- iii. mixed intercropping – growing two or more crops in no distinct row arrangement which is more typical of traditional agro-systems. As mentioned earlier, some text may not necessarily refer to this as a form of intercropping but rather ‘mixed cropping (Ruthenberg, 1971; Andrews and Kassam, 1975; Freyman and Venkateswarlu, 1977; cited in Willey, 1979) and,
- iv. relay intercropping – planting a second crop into a standing crop at a time when the standing crop is at its reproductive stage but before harvesting.

Willey (1979) stated that intercropping had long been recognized as a common agricultural practice in the tropics. This view was also shared by Walker (2009) who stated that, in the tropics, many of the traditional cropping systems comprised more than one crop growing in one field at any given time. However, despite this historical contribution, intercropping has mostly been regarded as a primitive practice. This has meant that there has been limited research on intercropping as opposed to the volumes of research done on sole crops. The status of intercropping as a farming practice is similar to that of NUS. They too form part of historical cropping systems that have been sidelined by research in favour of the major crops – rice, wheat, maize and potato.

### ***1.9.1 Resource Utilization***

Intercropping is known for its main advantage of allowing plants to efficiently utilise available resources of light, water and nutrients thence increasing productivity (Lithourgidis *et al.*, 2011). Component crops use natural resources differently and therefore make better overall use of them than when grown as sole crops (Willey, 1979). They are able to completely absorb and convert natural resources such as solar radiation, water and nutrients to crop biomass thus improve yield production. This is due to the fact that component crops have different competitive abilities for resources due to variation in crop characteristics such as rates of canopy development, final canopy size, photosynthetic adaptation of irradiance conditions and rooting depth (Midmore, 1993; Marris and Garrity, 1993; Tsubo *et al.*, 2001).

Radiation interception is perhaps the most important factor affecting productivity of intercrops. Since radiation intercepted depends on canopy size and duration (Black and Ong, 2000), this provides a scenario whereby it can be manipulated by varying plant density and spatial arrangements within the intercrop. Thus, selection of crops that differ in competitive ability in space or time is important (Lithourgidis *et al.*, 2011). Previous research has shown that intercropping is more efficient when component crops differ greatly in growth duration (Wien and Smithson, 1981; Smith and Francis, 1986; Fukai and Trenbath, 1993; Keating and Carberry, 1993). Rao and Willey (1980) found that intercropping late maturing pigeon pea with early maturing setaria improved the Land Equivalent Ratio (LER); LER is a measure of the efficiency of intercropping in relation to monocropping.

Intercropping has also been reported to improve water-use efficiency (WUE) (Hook and Gascho, 1988). It was reported to result in increases in WUE (18 - 99%) relative to WUE of sole crops of component crops (Morris and Garrity, 1993). In separate studies, Sani *et al.* (2011) observed better water-use in a maize-sorghum intercrop while Oseni (2011) observed it in a sorghum-cowpea intercrop. High leaf area and leaf area index have been identified as some of the factors which contribute to water conservation in intercropping (Ogindo and Walker, 2005). Morris and Garrity (1993) found that intercropping improved water capture by 7% compared with monocropping. Elsewhere, it was found that WUE of a maize-soybean intercrop was higher than that of sole crops (Barhom, 2001). As such, intercropping can be a very useful cropping practice in water scarce areas.



Differences in root and canopy architecture of component crops provides a platform for harnessing more solar radiation, improved water- and nutrient- use than root and leaves of a sole crop (Thayamini and Brintha, 2010). Dahmardeh *et al.* (2009) reported that maize-cowpea intercropping increased soil nitrogen, phosphorus, and potassium content in relation to a maize mono crop. Intercropping between high and low canopy crops can improve light interception and consequently yield (Azam-Ali *et al.*, 1990). In the case of this study, taro and bambara groundnut exhibit different canopy architecture, and size as well as different rooting depths. On one hand, taro is characterised by large leaves compared with the small leaves of bambara groundnut. In addition, taro plants grow taller than bambara groundnut plants. Lastly, taro has shallow roots while bambara groundnut has a deeper rooting system. Hypothetically, intercropping taro and bambara groundnut would create a scenario whereby the root density in the soil is increased. Increased root density implies enhanced soil water capture which would translate to greater biomass production.

### ***1.9.2 Sustainability***

Issues of sustainability have taken centre stage in most debates. As such, as we advocate for the promotion of NUS and alternative farming practices, such discussions should also focus on sustainability. Such sustainability should be long-term, enhance the environment as opposed to degradation and still meet the objective of feeding the human population. Here we will define ‘sustainability’ according to Sivakumar *et al.* (2000) who described sustainability as the balance between utilization to satisfy human needs and maintenance of the environment. Hansen (1996) also provides some useful definitions of sustainability that are specific to agriculture. Since sustainable agriculture seeks, in most cases, to mimic nature, intercropping offers a rare window to achieve such. Intercropping increases on-farm diversity maximizes on resource use and conversion to biomass as well as improving water- and nutrient-use. Other benefits of intercropping may also include reduced incidence of pests and disease in intercrops as well as reduced requirement for labour for weeding. This amounts to savings (financial and human resource) for resource-constrained farmers. Theoretically, this creates a balance between providing food and fibre for man, enhancing the environment and avoiding

environmental degradation. This implies that intercropping is indeed a sustainable farming practice.

### **1.10 Conclusion**

It is possible that the key to future food security may very well lay in the untapped potential of neglected underutilised crops. Therefore, it is imperative that we study locally available neglected underutilised crops and evaluate them for drought tolerance using agronomic techniques as well as recent techniques such as crop modelling, which allow for rapid evaluation of production scenarios. Since a crop's ability to tolerate drought is dependent on a complex or dynamic variety and combination of responses and mechanisms, the study sought to evaluate the dynamics of drought tolerance in selected landraces of taro and bambara groundnut, two crops that occupy the status of NUS within South Africa.

An understanding of morphological mechanisms involved in the responses of taro and bambara groundnut landraces is fundamental to their identification as drought tolerant crops. Such an understanding of morpho-anatomical responses would contribute significantly towards breeding for drought tolerance and making available developed varieties of these two NUS. The use of crop modelling as a technique may also aid in the interpretation of agronomic field data. Well-calibrated and validated models could also assist as selection tools for drought tolerance in these crops thus reducing on time and resources needed to fill the knowledge gap on these NUS.

### **1.11 Structure of thesis**

A series of agronomic and modelling experiments were conducted over two seasons (2010/11 and 2011/12) to answer the objectives of this study. This thesis consists of individual manuscripts, whereby each manuscript answers to a certain objective related to a particular crop:

**Chapter 2** is a short communication which serves as an introduction and a scientific description of the taro landraces used in this study. It details results of agro–morphological characterisation and DNA fingerprinting done using SSR primers. It also seeks to justify that the taro landraces used in this study were indeed different.

**Chapter 3** reports on field trials conducted at Ukulinga, Pietermaritzburg to determine drought tolerance mechanisms involved in taro. It answers the first objective of the study. It describes results of field trials such as emergence, stomatal conductance, chlorophyll content index, plant height, leaf number, leaf area index (LAI), vegetative growth index, yield and yield components as well as yield determinants.

**Chapter 4** reports on results of experiments conducted in a rainshelter at Roodeplaat, Pretoria to evaluate growth, yield and water–use of taro landraces under varying water regimes. These experiments were linked to the second objective of the study. It also reports on emergence, stomatal conductance, plant height, leaf number, LAI, destructive sampling (root length, fresh and dry mass), yield and yield components, water–use efficiency (WUE) and yield determinants of taro landraces.

**Chapter 5** comprises the first part of work done on bambara groundnut landraces to evaluate their growth and yield responses to water stress under field conditions at Roodeplaat, Pretoria. Similar to Chapter 3 on taro, this study also seeks to determine drought tolerance mechanisms associated with drought tolerance in bambara groundnut landraces. It reports on results of emergence, stomatal conductance, chlorophyll content index, plant height, leaf number, LAI, biomass, phenology (timing and duration of flowering, maturity and senescence), yield and yield components as well as yield determinants.

**Chapter 6** is a sequel to Chapter 5 and also reports on growth and yield responses of bambara groundnut landraces to water stress, using results from rainshelter experiments conducted at Roodeplaat, Pretoria. It relates to the second objective of the overall study. Results reported in this paper include emergence, stomatal conductance, chlorophyll content index, plant height, leaf number, LAI, biomass, phenology (timing and duration of flowering, maturity and senescence), WUE, yield and yield components as well as yield determinants.

**Chapter 7** is linked to the last objective of the whole study to evaluate the feasibility of intercropping taro and bambara groundnut landraces under dryland conditions in Umbumbulu, KwaZulu-Natal, South Africa. The aim was to evaluate if intercropping taro and bambara groundnut landraces, mainly studied as sole crops in this study, could be practised in rural areas as an alternative cropping system. The study also recognised that in these areas taro is the main crop grown as a cash crop. Therefore, the study evaluated if intercropping taro and bambara groundnut could be productive without causing significant yield losses to the farmers' main crop – taro. Results reported include emergence, plant height, leaf number, yield and yield components and land equivalent ratio (LER).

**Chapter 8** reports on the calibration and validation of the FAO's AquaCrop model for taro and bambara groundnut landraces from South Africa. It addresses the third objective of the overall study. Results from field and rainshelter trials, as well as other preliminary studies not included in the body of this thesis, were used to develop parameters for one landrace of taro and as well as one bambara groundnut landrace selection. Results from the first season (2010/11) were used to calibrate the model, while results from the second season (2011/12) were used for validation. Where available, independent data were also used to verify model applicability to different soils, climates and management.

**The general discussion** forms the last and final chapter of the study. It offers a holistic discussion, encompassing all the separate studies reported in this thesis. It also highlights on major findings, outcomes and implications of the study. This section winds up by offering concluding statements to the thesis as well as recommendations for future studies.

## **References**

**(See final reference list pages)**

## CHAPTER 2

### **Preliminary assessment of genetic diversity in three taro (*Colocasia esculenta* L. Schott) landraces using agro–morphological and SSR DNA characterisation**

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## **Abstract**

Taro (*Colocasia esculenta* (L.) Schott) is an important underutilised crop in South Africa, East Africa and Indonesia. Three taro landraces, namely, Dumbe Lomfula (wild), KwaNgwanase and Umbumbulu, were collected from two locations in KwaZulu-Natal (KZN), South Africa, and planted at two locations, Pietermaritzburg (KZN) and Roodeplaat, Pretoria. Agro-morphological characterisation of vegetative and corm characteristics were done four months after planting and at harvest, respectively. Sampling for DNA fingerprinting using five SSR primers was done using leaf material four months after planting. Agro-morphological characterisation was useful in showing differences between the wild landrace and the two cultivated landraces, as well as identification of dasheen and eddoe types. SSR primer characterisation showed that despite significant morphological differences, the wild Dumbe Lomfula and Umbumbulu landraces were closely related but different from the KwaNgwanase landrace. Although landraces showed great morphological variation, this did not necessarily imply genetic variation. It is concluded that SSR primers are more useful for characterising taro landraces.

*Keywords:* agro-morphology, characterisation, DNA, landraces, SSR primers, taro (*Colocasia esculenta* L. Schott), genetic diversity

## **1. Introduction**

Taro [*Colocasia esculenta* (L.) Schott] is a major root crop belonging to the family *Araceae*, sub-family *Aroideae* (Lebot, 2009). It is one of the oldest crops known to man and is thought to have originated from tropical America and Asia (Lebot, 2009). The spread of taro into Africa may have been through the Mediterranean (Léon, 1977; Purseglove, 1979; Plucknett, 1984), reaching Egypt about 2000 BC (Plucknett et al., 1970). From there, it may have spread to the rest of Africa through trade and migration. Taro is one of the few edible species in the genus *Colocasia* (Ezumah, 1972) and is the most widely cultivated species (Vinning, 2003). In South Africa, taro is a traditional crop locally called “*amadumbe*” in the

Zulu vernacular and is generally consumed as a subsistence crop (Shange, 2004), although its commercialisation has recently occurred in Umbumbulu, a rural district of KwaZulu-Natal (Modi, 2003). The name “*amadumbe*” derives from the fact that taro is most common in coastal areas and the hinterland of KwaZulu-Natal province (Modi, 2004) starting at Bizana district in the Eastern Cape and the rest of coastal KwaZulu-Natal. The crop is also cultivated, to a lesser extent, in the sub-tropical and tropical regions of Mpumalanga and Limpopo provinces (Shange, 2004). With improved information availability, taro production as well as its commercialisation may be expanded. However, such expansion is limited, in part, by the lack of improved cultivars. Subsistence farmers currently rely on landraces selected over generations to suit their agro-ecological and social requirements (Singh et al., 2008). Very little is known of the genetic diversity that exists in these local landraces.

Shange (2004) and Mare (2006) morphologically characterised local taro landraces in KwaZulu-Natal, however, they primarily focussed on eddoe types. While morphological characterisation may show variation, this may not necessarily reflect variation at the molecular level (Okpul, 2005; Singh et al., 2008). As such, there is a need for molecular characterisation, in addition to morphological characterisation, in order to determine the full nature and extent of differences. Within South Africa, there have been no reported efforts to characterise local landraces using molecular markers. Singh et al. (2008) evaluated 859 accessions from Papua New Guinea (using 30 agro-morphological descriptors) and DNA fingerprinting [using seven simple sequence repeats (SSR) primers]. Previously, other researchers had used DNA fingerprinting techniques such as amplified fragment length polymorphism (AFLP) primers (Quero-Garcia et al., 2004), and random amplified polymorphic DNA (RAPD) primers (Singh et al., 2011) to characterise taro. However, SSR primers were regarded to be advantageous over AFLP and RAPD (Hamza et al., 2004). Therefore, the aim of this study was to characterise genetic diversity in three taro landraces from KwaZulu-Natal, South Africa, using agro-morphological characterisation and DNA fingerprinting using five SSR primers.

## 2. Materials and methods

### 2.1 Plant material and experimental design

Three taro landraces were collected from two locations in KwaZulu-Natal (KZN); one from KwaNgwanase (KW) (27°1'S; 32°44'E) in northern KZN, and two from Umbumbulu [UM and Dumbe Lomfula (DL): 29°36'S; 30°25'E] near the south coast of KZN (Figure 1). Table 1 detailed the background information on the landraces as well as existing knowledge describing the agronomy of the landraces. All landraces were planted using corms (Figure 1) in a randomised complete block design (RCBD) replicated three times, at two locations – Pietermaritzburg, KZN (29°37'S; 30°16'E; 775 masl) and Roodeplaat, Pretoria (25°60'S; 28°35'E; 1 168 masl), during the summer of 2010/11.



**Figure 1:** An illustration of the three taro landraces (A – Dumbe Lomfula; B – KwaNgwanase; C – Umbumbulu) in their natural habitats (A1, A2 & A3) and the shapes of their corms or cormels (B1-3). Note the differences in corm shapes as well as natural habitats of the three landraces.



## ***2.2 Agro-morphological characterisation***

Agro-morphological characterisation was done when plants had reached their maximum vegetative stage (four months after planting). A total of 17 plant characteristics, split into vegetative and corm characteristics, were used to characterise the landraces as described by the International Network on Edible Aroids (INEA) (<http://www.ediblearoids.org>). The parameters, both quantitative and qualitative, included descriptions of vegetative growth (stolon formation, plant height, shape of lamina, orientation of lamina, leaf lamina margin, lamina colour, variegation of lamina, sinus, vein junction, colour of leaf petiole, variation on petiole, flowering, maturity) and corm characteristics (corm shape, weight, flesh colour, eating quality). An average value, of 6 plants, was used to describe quantitative traits.

## ***2.3 SSR characterisation***

Leaf samples of the three taro landraces taken during the maximum vegetative period were used for DNA extraction and SSR characterisation. DNA was isolated using the CTAB (cetyl trimethyl ammonium bromide) method (Murray and Thompson, 1980). Agarose (3%) gel electrophoresis and spectrophotometry were used to determine the integrity and concentrations of DNA. Based on previous assays of amplification and product length polymorphism in taro landraces, five SSR primers (Mace and Godwin, 2002) were used.

Polymerase chain reaction (PCR) amplification was performed in 0.2 mL plates using an MJ-Research PTC-100® thermal cycler. The PCR reaction mixture (10 µL) contained in 10 ng template DNA, 0.24 µM each of forward and reverse primers, 0.4 mM of each dNTP, 3.5 mM MgCl<sub>2</sub>, 0.75 U TAQ DNA polymerase and 1 µCi [ $\alpha$ -<sup>32</sup>P] dATP. The PCR regime consisted of an initial denaturation (94 °C for 5 min), 35 cycles each consisting of 30 sec denaturation (94 °C), 1 min annealing (ranging from 62 – 65 °C) (Table 2). Thereafter, the amplified products were mixed with 5 µL stop solution [98% formamide, 10 mM EDTA, 0.05% (w/v)] xylene cyanol and 0.05 bromophenol blue) and denatured at 94 °C for 3 min. A 2 µL aliquot was loaded onto denaturing polyacrylamide gels (10% acrylamide/bisacrylamide 19:1) and electrophoresed.

## **Tables**

**Table 1.** General information on the three taro landraces [KwaNgwanase (KW), Umbumbulu (UM) and Dumbe Lomfula (DL)]. The information provides a brief description of the place where the landrace was sourced from, its natural habitat or place of cultivation as well as a summary of current existing knowledge on the landrace.

<b>Description of locations where landraces were sourced</b>				<b>Existing knowledge of landraces</b>			
<b>Area of Location</b>	<b>Coordinates</b>	<b>Altitude (masl) †</b>	<b>Climatic description</b>	<b>Local Name</b>	<b>Landrace type</b>	<b>Growing conditions</b>	<b>Assumed drought tolerance</b>
Umbumbulu (UM)	29°36'S; 30°25'E	Lowlands (< 500 m)	Semi-arid	Dumbe dumbe	Eddoe	Cultivated - upland (slopes)	Unknown
Umbumbulu (DL)	29°36'S; 30°25'E	Lowlands (< 500 m)	Semi-arid	Dumbe Lomfula	Dasheen	Wild - shallow rivers	Unknown
KwaNgwanase (KW)	27°1'S; 32°44'E	Lowlands (< 500 m)	Humid	Phondo	Dasheen	Cultivated - Swamps	Unknown

†Note masl = meters above sea level.

**Table 2.** Profiles of five SSR primers used for molecular characterisation of three taro landraces (DL, KW & UM).

<b>SSR ID</b>	<b>Sequence</b>	<b>bp<sup>†</sup></b>	<b>Annealing Temp (°C)</b>
Uq55-112 F	<sup>‡</sup> Fwd: CTT TTG TGA CAT TTG TGG AGC	21	
Uq55-112 R	<sup>§</sup> Rvs: CAA TAA TGG TGG TGG AAG TGG	21	62
Uq73-164 F	Fwd: ATG CCA ATG GAG GAT GGC AG	20	
Uq73-164 R	Rvs: CGT CTA GCT TAG GAC AAC ATG C	22	65
Uq84-207 F	Fwd: AGG ACA AAA TAG CAT CAG CAC	21	
Uq84-207 R	Rvs: CCC ATT GGA GAG ATA GAG AGA C	22	65
Uq88B-94 F	Fwd: CAC ACA TAC CCA CAT ACA CG	20	
Uq88B-94 R	Rvs: CCA GGC TCT AAT GAT GAT GAT G	22	62
Uq110-283 F	Fwd: AGC CAC GAC ACT CAA CTA TC	20	
Uq110-283 R	Rvs: GCC CAG TAT ATC TTG CAT CTC C	22	65

<sup>†</sup>Note bp = number of base pairs; <sup>‡</sup>Fwd = forward primer; <sup>§</sup>Rvs = reverse primer.

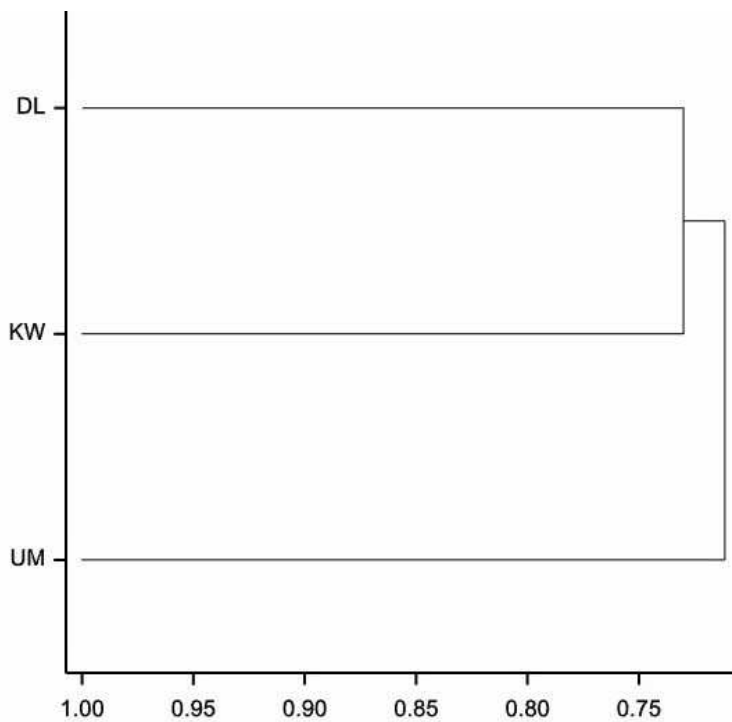
#### **2.4 Data analysis**

For each of the three taro landraces, band positions and primer combinations were scored using photographic prints of electrophoresis gels. Scores were entered as either present (score = 1) or absent (score = 0). Scores were then analysed using hierarchical cluster analysis in GenStat® (Version 14, VSN, UK) and dendrograms of the genetic relatedness of the three landraces produced.

### 3. Results and discussion

#### 3.1 Morphological characterization

Results of morphological characterisation (Table 3) were based on a set of 17 parameters, split into vegetative and corm characteristics. Cluster analysis of agro-morphological characteristics grouped landraces into two distinct groups at a similarity index of 0.73 (Figure 2). The first group comprised Dumbe Lomfula and KwaNgwanase landraces, while the second group consisted of Umbumbulu. Dumbe Lomfula and KwaNgwanase landraces were dasheen type landraces characterised by a single central corm and several, small, side cormels which are not edible (Lebot, 2009). The similarity index between Dumbe-Lomfula and Umbumbulu landraces was only 0.22 (Figure 2). This was because the Umbumbulu landrace was an eddoe type landrace characterised by numerous cormels which form the edible part (Lebot, 2009).



**Figure 2:** Dendrogram illustrating genetic relatedness of the three taro landraces generated by hierarchical cluster analysis using GenStat® from scores of the 17 agro-morphological parameters. Note: DL = Dumbe Lomfula, KW = KwaNgwanase and UM = Umbumbulu.

**Table 3.** Agro–morphological characterisation of three taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) and Umbumbulu (UM)] collected from KwaZulu-Natal, South Africa.

<b>Descriptor</b>	<b>Dumbe Lomfula (DL)</b>	<b>KwaNgwanase (KW)</b>	<b>Umbumbulu (UM)</b>
Vegetative			
1. Stolon formation	Stolons only	Partly present	Absent
2. Suckers formation	Absent	Partly present	Suckers only
3. Plant height	Very tall (> 150 cm)	Tall (100-150 cm)	Medium (50-100 cm)
4. Orientation of lamina	Tip-pointing downwards	Semi-horizontal	Semi-horizontal
5. Leaf lamina margin	Undulated narrow	Undulated narrow	Entire
6. Lamina colour	Normal green	Normal green	Normal green
7. Variegation of lamina	Absent	Absent	Absent
8. Sinus	Narrow pointed	Narrow pointed	Narrow pointed
9. Leaf petiole colour	Brown-purple	Light purple	Light green
10. Vein junction	Light purple	Light green	Dark purple
11. Variation of petiole	None	None	Upper part darker
12. Flowering	Rarely flowering	Never flowering	Never flowering
Corm characteristics			
13. Maturity	Very late (> 10 months)	Late (8-10 months)	Intermediate (6-8 months)
14. Corm shape	Cylindrical	Elliptical	Conical
15. Corm mass	Large (2-4 kg)	Medium (0.5-2 kg)	Very small (< 0.25 kg)
16. Flesh colour	White	White	Greyish-white
17. Eating quality	Good	Very good	Very good

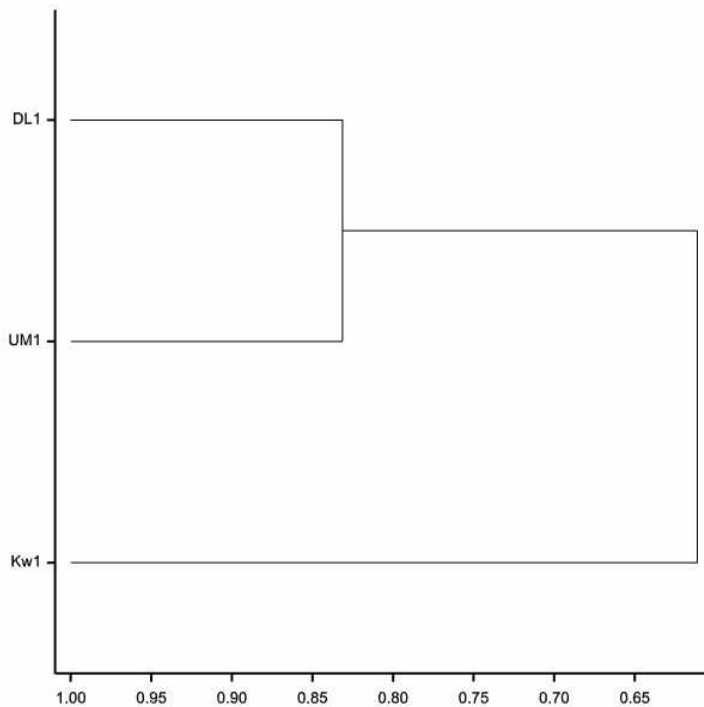
Among the landraces, large variations were observed for morphological characteristics such as stolon and/or sucker formation, plant height, leaf petiole and vein junction colour, and corm shape (Table 3). On average, the Dumbe Lomfula and KwaNgwanase landraces had evidence of stolon formation; the two landraces also had relatively tall plants (> 1 m) and very large leaves relative to the Umbumbulu landrace. The Umbumbulu landrace did not form stolons but rather had suckers, which was typical of eddoe type varieties (Table 3). Other characteristics such as corm mass and maturity also contributed to the variation between the landraces. Dumbe Lomfula and KwaNgwanase landraces formed large to medium sized corms while the Umbumbulu landrace formed small but numerous cormels (Table 3). In addition, the

Dumbe Lomfula landrace was a perennial crop while KwaNgwanase was a late maturing variety. Umbumbulu landrace, on the other hand, was shown to mature earlier relative to the other two landraces (Table 3). On the other hand, all landraces showed similarities with respect to sinus, lamina colour and variegation of the lamina.

Previous characterization of local landraces (Shange, 2004; Mare, 2006) had mainly focussed on eddoe type landraces to the exclusion of dasheen type landraces. This may be because the eddoe type landraces are more popular in KwaZulu-Natal, South Africa than dasheen type landraces. Such popularity may also be due to the fact that there currently exists a market for eddoe type landraces (Modi, 2003).

### ***3.1 SSR characterization***

Contrary to the results of morphological characterization, DNA fingerprinting using five SSR primers showed that Dumbe-Lomfula and Umbumbulu landraces were more similar (0.82) to each other, while the KwaNgwanase landrace was distinctly different (Figure 3). Morphological characterization had showed that the similarity index between Dumbe-Lomfula and Umbumbulu landraces was only 0.22 (Figure 2). The genetic similarity between the wild Dumbe Lomfula and cultivated Umbumbulu landrace may be due to the fact that the two landraces were collected from the same location (Table 1). Molecular characterisation did not show distinct differences between the two morphological groups, Dasheen and Eddoe landrace (Figure 3). This concurs with Lebot's (2009) statement that these two morphological groups are not differentiated by molecular markers. The author further suggested that eddoe types were less genetically improved and yielded less than dasheen types. This assertion concurred with morphological characterisation which showed that the eddoe type Umbumbulu landrace had smaller sized corms which weighed less than corms of the dasheen type landraces, Dumbe-Lomfula and KwaNgwanase.



**Figure 3:** Dendrogram illustrating the genetic relatedness of the three taro landraces generated by hierarchical cluster analysis using GenStat<sup>®</sup> from scores of the 5 SSR primers. Note: DL = Dumbe Lomfula, KW = KwaNgwanase and UM = Umbumbulu.

Furthermore, our results of DNA characterization (Figure 4) which showed that there were differences between the agro-morphological characterisation and SSR primer characterisation were consistent with earlier reports by Okpul et al. (2005) and Singh et al. (2008). In their separate studies (Okpul et al., 2005; Singh et al., 2008), they reported that molecular analyses did not often result in clusters similar to those of morphological traits. This agreed with our own observations whereby DNA characterization resulted in clusters (Figure 3) that were contrary to those derived using morphological characterization (Figure 2). They went on to state that, while morphological characterisation may show differences, such differences may not exist, entirely, at the genetic level and could be an outward expression imposed by genotype and environment interactions. In such cases, they suggested that molecular characterisation was more accurate compared with morphological characterisation.

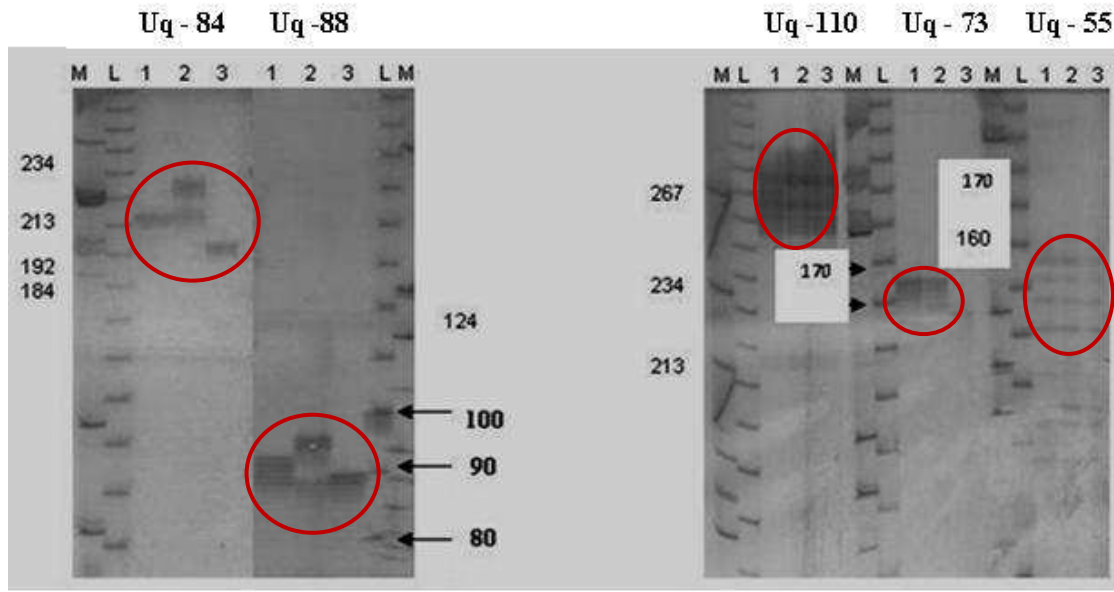


Figure 4: Levels of polymorphism observed for the five primers (Uq – 84, Uq -88, Uq – 110, Uq – 73 & Uq – 55). Note: M = Marker; L = 10 base pair ladder; 1 = Dumbe Lomfula, 2 = Umbumbulu and 3 = KwaNgwanase. Note that the numbers on the gels represent the sizes (in base pairs) of bands where areas of polymorphism (circled in red) occurred.

#### 4. Conclusion

Both agro-morphological and SSR primer characterisation were useful in identifying differences between landraces. Morphological characterisation was able to show differences between the dasheen and eddoe types, which were not clear at the molecular level. Agro-morphological characterisation suggested that the wild Dumbe Lomfula landrace and the cultivated KwaNgwanase, both dasheen types, were similar. However, SSR primer characterisation showed that Dumbe Lomfula and Umbumbulu landraces were more similar while the KwaNgwanase landrace was different from them. The extent of genetic diversity within the taro landraces may be confined to geographic location than morphology. There is need for further research to collect and analyse, using SSR primers, all landraces of taro occurring in South Africa.



## **Acknowledgements**

Water Research Commission of South Africa K5/177/4 Water-Use of Drought Tolerant Crops. WRC Knowledge Review 2008-09.

## **References**

**(See final reference list pages 198-228)**

## CHAPTER 3

### **Drought tolerance of selected taro (*Colocasia esculenta* L. Schott) landraces from KwaZulu-Natal, South Africa**

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## **Abstract**

Growth, phenological, yield and drought mechanisms of three taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) and Umbumbulu (UM)] were evaluated under field conditions (irrigated and rainfed) at Ukulinga Research Farm, Pietermaritzburg, South Africa, over two summer seasons. Emergence, plant height, leaf number, leaf area index (LAI), stomatal conductance (SC) and chlorophyll content index (CCI) were determined. Vegetative growth index (VGI) was also calculated. Biomass, yield and harvest index (HI) were determined at harvest. Taro was slow to emerge (~ 49 days) and showed significant differences between landraces with respect to final emergence with DL never achieving a good crop stand. Growth (plant height, leaf number and LAI), VGI, SC and CCI were significantly lower under rainfed than irrigated conditions. Rainfed conditions resulted in significantly lower biomass, HI, and final yield of taro landraces compared to irrigated conditions. The DL landrace failed to produce any yield. The UM landrace showed better adaptations to water stress compared with the KW and DL landraces. The UM landrace avoided drought through increased stomatal regulation, lowering chlorophyll content, smaller canopy size and reduced growth period. It is concluded that among the three landraces, UM is suitable for production under water stress conditions, because it exhibited drought avoidance and escape mechanisms.

**Key words:** Drought, landrace, LAI, stomatal conductance, chlorophyll, vegetative growth index, yield.

## INTRODUCTION

Current reports suggest that world population is going to reach 9 billion by 2050 (United Nations, 2009) and that the world's current staple crops (maize, rice and wheat) will not be able to meet demand for food (Baye et al., 2001). This creates a quagmire – how to feed all these people? The challenge has sparked recent interest in the possible use and re-introduction of neglected underutilised species (NUS) (Mabhaudhi, 2009). Azam-Ali (2010) defined NUS as crops that were previously not classified as major crops, have been under-researched and currently occupy low levels of utilisation, and are mainly confined to small-scale farming areas. Unlike most staple crops, most NUS crops are believed to be adapted to a range of ecological niches (Padulosi, 1998), which are often marginal and harsh, thus offering sustainable food production (Idowu, 2009). Such crops include taro [*Colocasia esculenta* (L.) Schott], locally known as *Amadumbe* in South Africa.

Taro is thought to be one of the oldest domesticated crops, with a history of cultivation in the Indo-Pacific dating back to more than 10, 000 years (Cable, 1984; Plucknet, 1984; Haudricourt and Hédin, 1987 cited in Lebot, 2009; Rao et al., 2010). In South Africa, taro is an important NUS cultivated by subsistence farmers using landraces. Its production remains confined to mostly rural coastal areas of KwaZulu-Natal and the Eastern Cape provinces (Shange, 2004). Over the last decade, semi-commercialisation of taro by subsistence farmers (Modi, 2003; Agargaad and Birch-Thomsen, 2006) has contributed to an increase in taro production. As such, there is growing interest to promote it among small-scale farmers in other parts of the country, which may be drier than the coastal areas. Lack of scientific information describing effects of drought on growth, development and yield of diverse taro landraces remains a bottleneck to its successful expansion.

There has been limited research on drought tolerance of this crop. Snyder and Lugo, (1980) reported that drought tolerance existed in some wild relatives of taro, suggesting it was possible to develop drought tolerant hybrids. Sivan (1995) evaluated effects of drought on growth of two taro varieties (dasheen and eddoe) and tannia and observed that stomatal conductance declined under water stress relative to the well-watered treatment. In addition, water stress was shown to reduce leaf number and leaf area of both cultivars. In India, Sahoo et al. (2006), using taro hybrids, reported significant variations for taro growth parameters

such as height, leaf number and leaf area, leaf relative water content, chlorophyll stability index and injury by desiccation in response to osmotic stress. They further concluded that development of drought tolerant varieties of taro was a possibility after observing tolerance to osmotic stress with negligible yield reduction in the taro hybrid.

South Africa's research efforts on taro have primarily focussed on propagule quality and storage (Shange, 2004; Modi, 2007), with limited research on growth, and yield quality (Mare, 2006, 2010; Modi, 2007; Mare and Modi, 2012) as well as nutritional quality (McEwan, 2008). There has been no research describing taro's drought tolerance and there are currently no improved varieties of taro, hence local subsistence farmers still use landraces. Availability of information describing drought tolerance in these landraces could lead to development of drought tolerant varieties. It is hypothesised that local taro landraces may have developed drought tolerance over centuries of farmer and natural selection. Therefore, this study is aimed to evaluate the growth responses to water stress and mechanisms of drought tolerance of local taro landraces.

## **MATERIALS AND METHODS**

### **Planting material**

Three landraces of taro (*Amadumbe*) were collected from two locations in KwaZulu-Natal (KZN); one from KwaNgwanase (KW) (27°1'S; 32°44'E) in northern KZN, and two from Umbumbulu [UM and Dumbe Lomfula (DL): 29°36'S; 30°25'E] in the midlands of KZN, in April, 2010. The KW and DL landraces were classified as dasheen types characterised by a large central corm and no side cormels (Shange, 2004). The DL landrace was obtained from the wild where it was growing in shallow streams. The KW landrace was semi-domesticated and cultivated on stream-banks. The UM landrace is an upland landrace and is an eddoe type landrace characterised by a central corm and numerous side cormels which are the edible parts (Lebot, 2009). In order to eliminate propagule size effects, planting material was initially selected for uniform plant size (Singh *et al.*, 1998). Propagules were then treated with a bactericide and fungicide (Sporekill<sup>®</sup>) to prevent rotting during sprouting. Thereafter, propagules were sprouted in vermiculite (30°C, 90% RH) for 21 days before being planted out

in the field. KwaNgwanase was propagated using head-setts (huli), Umbumbulu and DL using sprouted corms and cuttings, respectively.

### **Description of experimental sites**

Field trials were conducted at the University of KwaZulu-Natal's Ukulinga Research Farm, Pietermaritzburg (29°37'S; 30°16'E) during the summer planting seasons of 2010/11 and 2011/12. Ukulinga represents a semi-arid environment and is characterised by clay-loam soils (USDA taxonomic system). Weather parameters were monitored by an automatic weather station (AWS) (ARC – Institute for Soil, Climate and Water) situated within a 100 m radius of the trials.

### **Experimental designs**

A factorial experiment with a split-plot layout arranged in a completely randomised block design was used at both experimental sites. Irrigation [full irrigation (FI) versus rainfed (RF)] was the main factor, while landrace type (DL, KW and UM) was the sub-factor. The sub-factor was replicated three times. The trials were planted on an area of 499.8 m<sup>2</sup>. Main plots measured 207.4 m<sup>2</sup> each, with 15 m spacing between them to prevent water from sprinklers in the FI treatment from reaching RF plots – sprinklers had a maximum range of 6 m radius. The sub-plot size was 17 m<sup>2</sup> with an inter-plot spacing of 1 m, and plant spacing of 1 x 0.5 m, translating to 20 000 plants per hectare. Irrigation scheduling for the full irrigation treatment was based on ET<sub>o</sub> from the AWS and was applied using sprinklers on 1 m high risers. In order to allow for maximum possible crop stand, the RF treatment was established under irrigation until plants had reached 90% emergence. Thereafter, irrigation was withheld from the RF treatment.

## **Agronomic practices**

Prior to commencement of trials, soil samples were taken for soil fertility and textural analysis. Results of soil texture analysis were used to define soil physical parameters of field capacity (FC), permanent wilting point (PWP) and saturation ( $K_{sat}$ ) using the Soil Water Characteristics Hydraulic Properties Calculator (<http://hydrolab.arsusda.gov/soilwater/Index.htm>). Land preparation involved disking and rotovating the fields to achieve a fine seedbed. Fertiliser was applied using an organic fertiliser, Gromor<sup>®</sup>, at a rate of 5 330 kg ha<sup>-1</sup> (Mare, 2010). Since taro takes long to mature, fertiliser application was split into two: half at planting and the remainder 20 weeks after planting, to ensure nutrient availability throughout the trials. Weeding and ridging were done by hand-hoeing.

## **Data collection**

The experimental designs and data collection were specifically designed to collect empirical data and observations for taro, which could later be used to model taro using AquaCrop (Steduto *et al.*, 2009). Data collection included emergence until at least 90% of the plants had emerged. Canopy characteristics [plant height, leaf number and leaf area index (LAI)] were determined starting from when the plants had reached 90% emergence. Plant height was measured from the bottom of the plant up to the base of the 2<sup>nd</sup> youngest fully unfolded leaf. Leaf number was counted only for fully unfolded leaves with at least 50% green leaf area. Leaf area index was measured using the LAI2200 Canopy Analyser (LI-COR, Inc. USA & Canada). During the 2010/11 season, only the KW and UM landraces were measured since the crop stand in the DL landrace was too low to allow good measurements to be taken. Stomatal conductance (SC) was determined using a steady state leaf porometer (Model SC-1, Decagon Devices, USA). During 2011/12 planting season, leaf chlorophyll content index (CCI) was determined using a chlorophyll content meter (CCM-200 *PLUS*, Opti-Sciences, USA). Stomatal conductance (SC) and CCI were measured from the abaxial and adaxial leaf surfaces, respectively, of the 2<sup>nd</sup> youngest fully unfolded leaf for the entire duration of the trial as described for SC by Sivan (1995). Soil water content (SWC) was monitored weekly using a

PR2/6 profile probe connected to a handheld HH2-moisture meter (Delta-T Devices, UK). The vegetative growth index (VGI) was measured in field trials as described by Lebot (2009) with minor modifications (Equation 1):

$$\text{VGI} = [((\text{leaf width} \times \text{leaf length}) \times \text{leaf number}) \times \text{H}/100] - (\text{suckers} + \text{stolons})^2 \quad \text{Equation 1}$$

where VGI = vegetative growth index

H = plant height

### **Statistical analysis**

Data collected from all trials were analysed using analysis of variance (ANOVA) with GenStat<sup>®</sup> (Version 14, VSN International, UK). Thereafter, least significant differences (LSD) were used to separate means at the 5% level of significance.

## **RESULTS**

### **Weather data**

Weather parameters (mean Tmax, Tmin, Rainfall and ET<sub>o</sub>) were measured for the duration of the trials (September to June in 2010/11 and 2011/12) (Fig 1). During the first season (2010/11), the average temperature was 19.5°C, with measured total rainfall of 939.2 mm against a calculated reference evapotranspiration (ET<sub>o</sub>) of 878.1 mm. As such, rainfall received during this period was greater (by 61.1 mm) than ET<sub>o</sub>. Based on monthly rainfall totals, rainfall was well distributed over the season. Most of the rainfall was received during the vegetative periods (Dec-March) and generally exceeded or matched ET<sub>o</sub> (Fig 1). During the 2011/12 season, the average temperature was similar to that of 2010/11, however, total rainfall (647.2 mm) received in 2011/12 was less than that received in the previous season.



Furthermore, total rainfall received was less (280.6 mm) than  $ET_o$ , suggesting that the crop may have suffered evaporative demand stress during the 2011/12 season. Lastly, rainfall distribution showed that rainfall during the whole growing season was lower than  $ET_o$ , except for March and November (Fig 1).

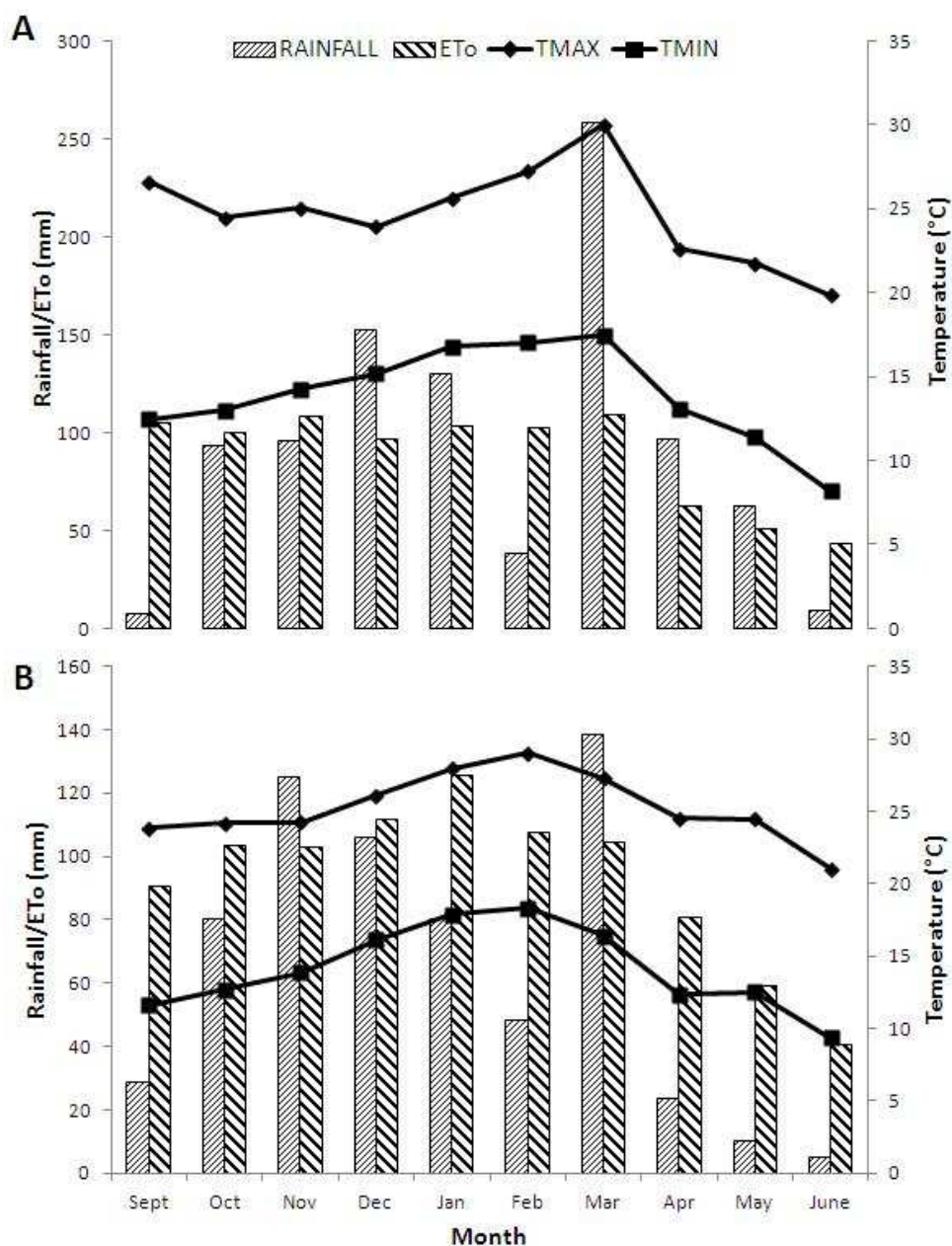


Figure 1: Maximum (Tmax) and minimum (Tmin) temperatures, rainfall and reference evapotranspiration ( $ET_o$ ) recorded at Ukulinga (Sept – June) during A. 2010/11 and B. 2011/12 planting seasons. Note the difference in rainfall and ( $ET_o$ ) recorded during 2011/12.

## Crop establishment

In order to allow for maximum possible crop stand, trials (irrigated and rainfed) were established under full irrigation. Irrigation was withdrawn when plants had reached at least 90% emergence. Results presented here show differences between landraces for both planting seasons. Taro landraces emerged slowly during the first 21 days after planting (DAP). Thereafter, emergence proceeded relatively faster, reaching 90% establishment at about 49 DAP, on average (Fig 2). Results of emergence showed highly significant differences ( $P < 0.001$ ) between landraces, with KW emerging faster compared to the UM and KW landraces. The DL landrace showed the lowest emergence, failing to reach 25% emergence throughout the season (Fig 2).

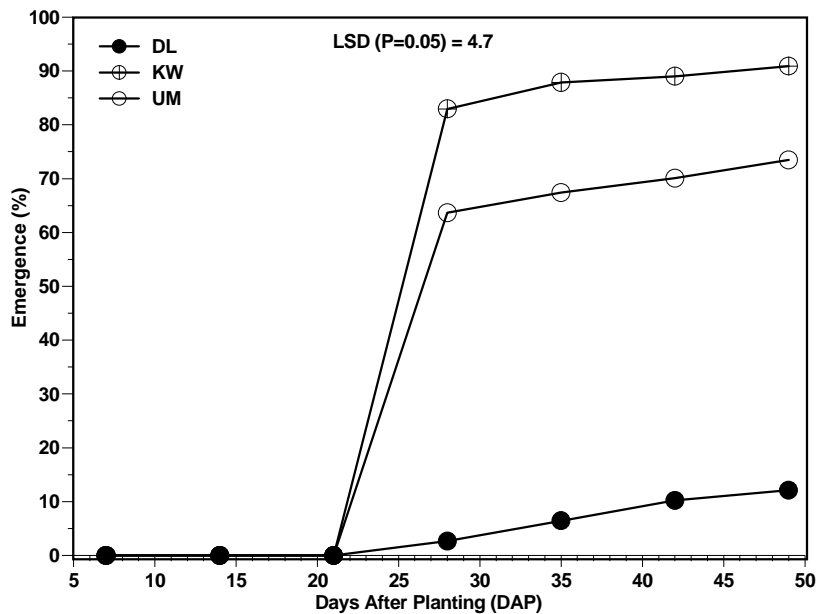


Figure 2: Emergence of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] based on mean values for both seasons. Note that DL was slow to emerge.

## Stomatal conductance and chlorophyll content index

Stomatal conductance (SC) was measured at the onset of the rapid vegetative stage (4 months after planting). Across both seasons, results showed highly significant differences ( $P < 0.001$ ) between irrigation treatments and landraces (Fig 3). During the 2010/11 season, there was a significant interaction ( $P < 0.05$ ) between irrigation treatments while in the subsequent season (2011/12), the interaction was not significant. Stomatal conductance was lower under rainfed, after 17 weeks, compared to irrigated conditions: it was almost twice as high under irrigated relative to rainfed conditions (Fig 3). On average, for both irrigation treatments, the DL landrace had higher SC than the UM landrace. Under rainfed conditions, based on mean values for both seasons, SC for DL, KW and UM was 34%, 52% and 58% lower, respectively, compared with irrigated conditions. Under rainfed conditions, the UM landrace was shown to have the lowest SC compared to the DL and KW landraces, suggesting a greater degree of stomatal control in the UM landrace.

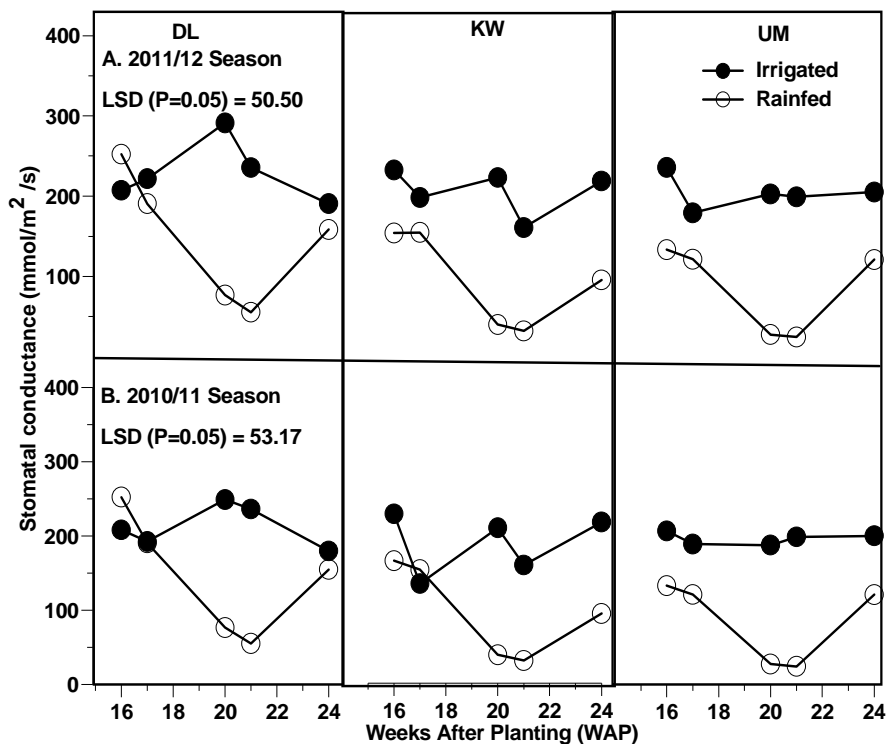


Figure 3: Stomatal conductance of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] grown under irrigated and rainfed conditions at Ukulinga during (b) 2010/11 and (a) 2011/12 planting seasons.

The trend in chlorophyll content index (CCI) was in line with observations of SC (Fig 3). Chlorophyll content index was shown to decrease significantly ( $P < 0.001$ ) under rainfed relative to irrigated conditions (Fig 4). Based on mean values, CCI was about 40% lower under rainfed compared with irrigated conditions. Landraces were shown to differ significantly ( $P < 0.001$ ) with respect to CCI. The UM landrace had the highest CCI compared with KW and DL landraces, respectively, under both irrigated and rainfed conditions. Results of CCI showed that DL had the greatest decrease (49%) while KW and UM had similar decreases (36%) under rainfed relative to irrigated conditions. This meant that, even though the UM landrace had lower CCI under rainfed conditions; it retained a higher CCI under rainfed (stress) conditions than the DL and KW landraces.

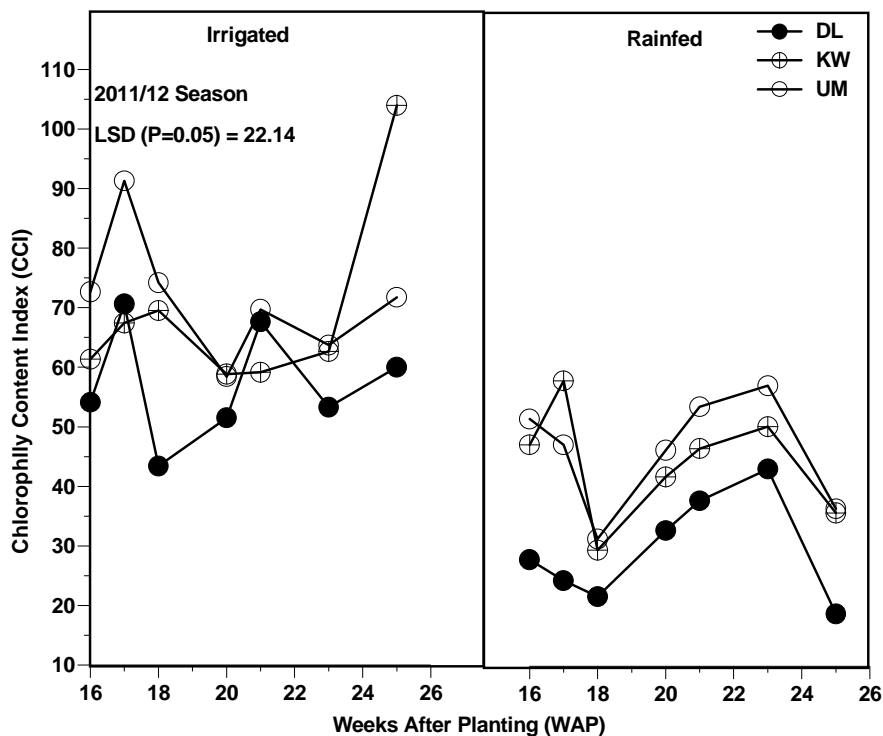


Figure 4: Chlorophyll content index (CCI) of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] grown under (a) irrigated and (b) rainfed conditions at Ukulinga during the 2011/12 planting season.

## Crop growth

Results collected from both seasons (2010/11 and 2011/12) showed that measured growth parameters of plant height, leaf number and LAI were negatively affected by limited water availability under rainfed conditions. Plant height results for both seasons recorded highly significant differences ( $P < 0.001$ ) between irrigation treatments, landraces and their interaction (Fig 5). Based on mean values of irrigated plots, DL had the tallest plants (117 cm) compared with KW (107 cm) and UM (82 cm), respectively. During 2010/11, plant height of KW, UM and DL was respectively 42%, 32% and 29% lower under rainfed relative to irrigated conditions. While for the subsequent season (2011/12), plant height of UM, KW and DL was respectively 33%, 31% and 26% lower under rainfed relative to irrigated conditions. Results showed that UM and KW landraces were more inclined to attain a lower maximum plant height under water limited conditions.

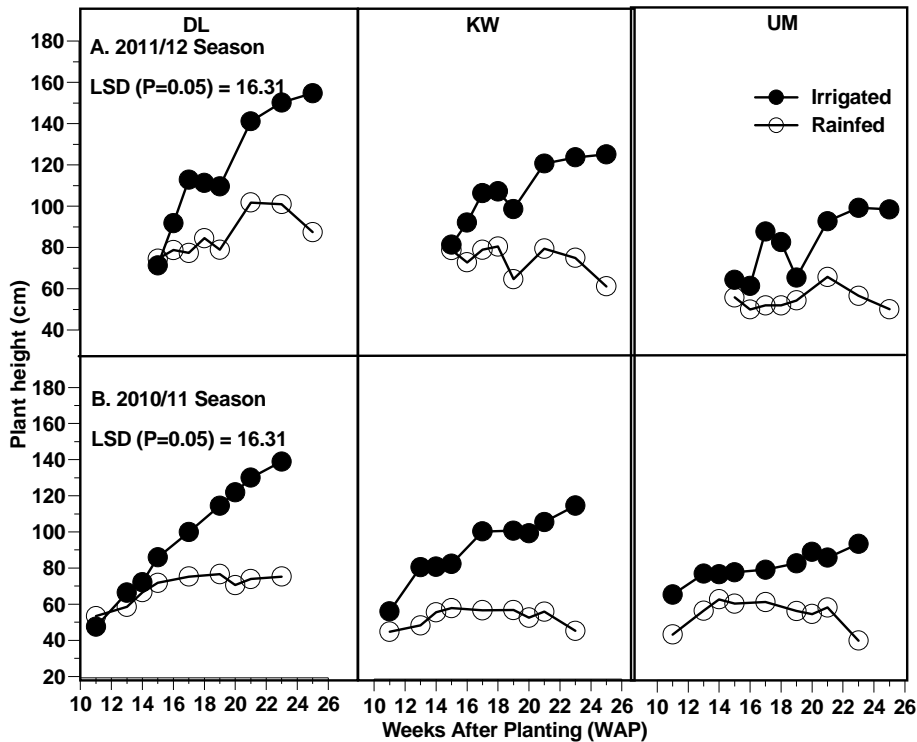


Figure 5: Plant height (cm) of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] grown under irrigated and rainfed conditions at Ukulinga during (b) 2010/11 and (a) 2011/12 planting seasons.

Results of leaf number measured for both seasons showed highly significant differences ( $P < 0.001$ ) between irrigation treatments and landraces. During the 2011/12 planting season there was a highly significant ( $P < 0.001$ ) interaction between irrigation treatments and landraces (Fig 6). Leaf number was, on average, higher during the 2011/12 season than the 2010/11 season although less rainfall was received during the former season. The observed trend of results, across both seasons, showed that, on average, DL and KW landraces had a higher leaf number than the UM landrace. Leaf number was shown to be consistently lower under rainfed relative to irrigated conditions. On average, for both seasons, leaf number of DL, KW and UM landraces was lower by 29%, 36% and 28%, respectively, under rainfed relative to irrigated conditions. The KW landrace had the greatest decrease in leaf number compared to the DL and UM landraces. This was consistent with lower plant height observed in the KW landraces under rainfed conditions.

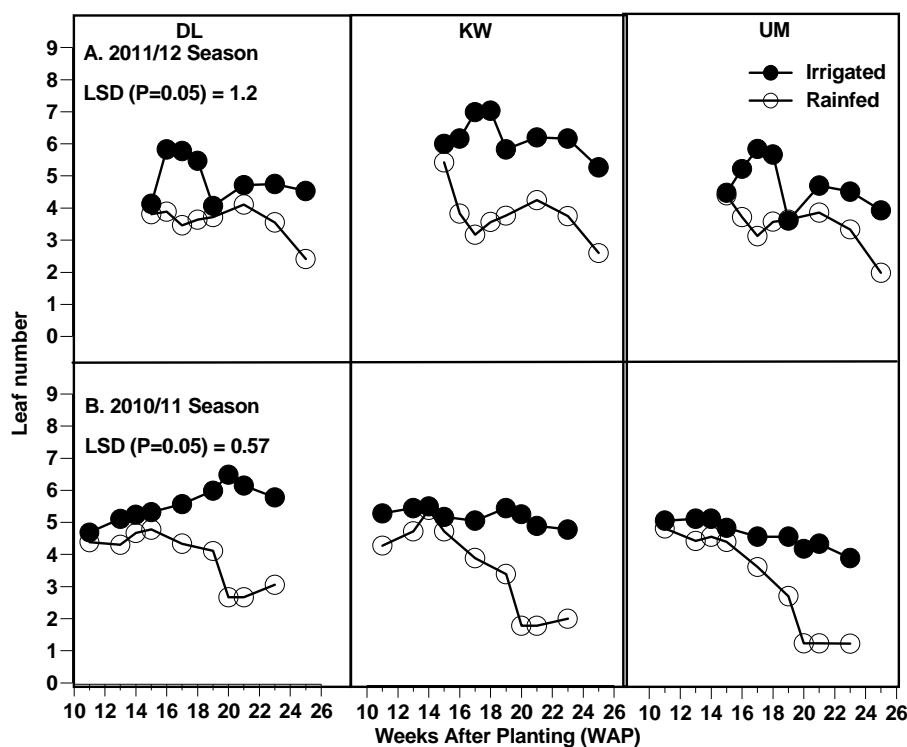


Figure 6: Leaf number of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] grown under irrigated and rainfed conditions at Ukulinga during (b) 2010/11 and (a) 2011/12 planting seasons.

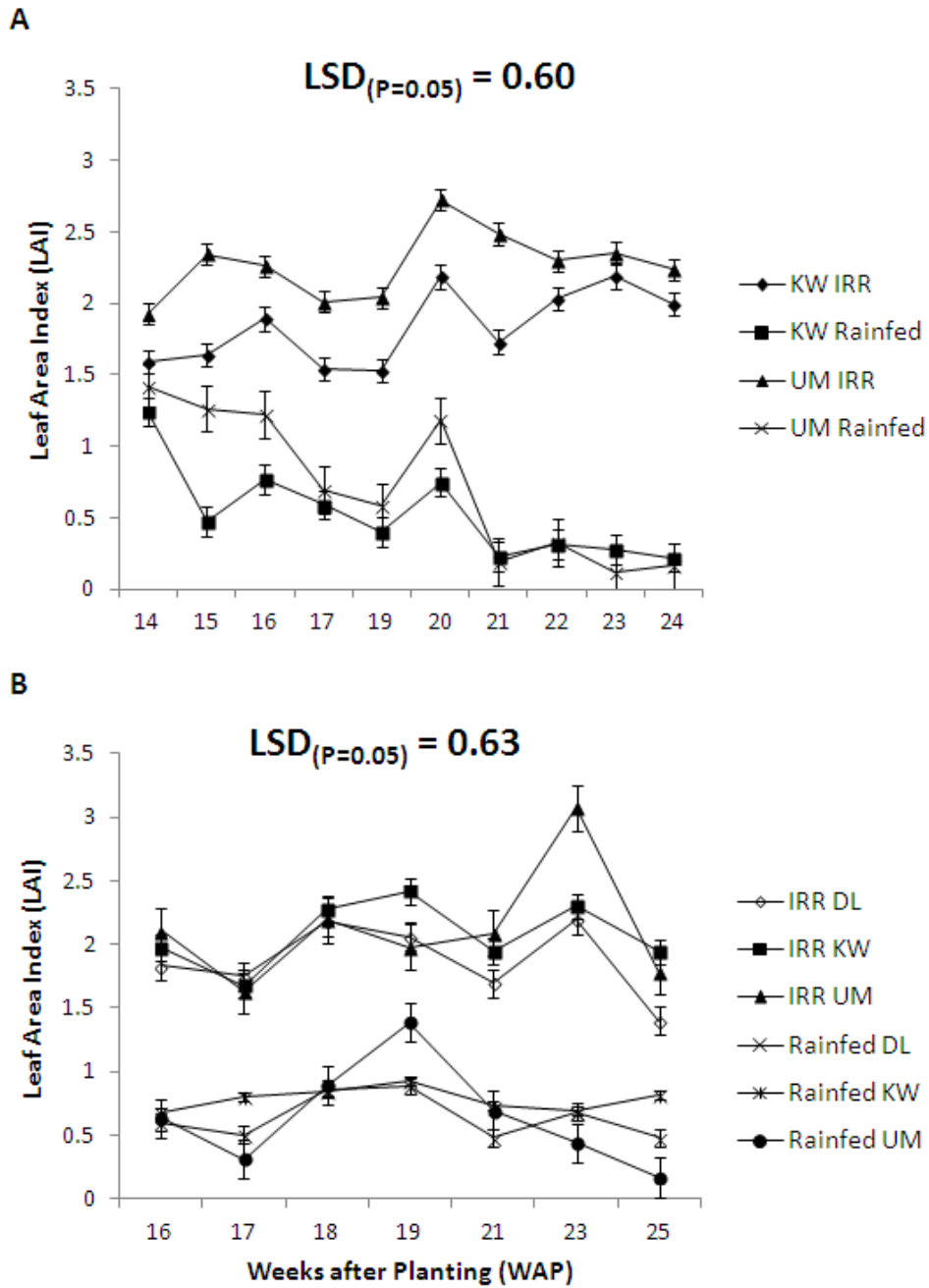


Figure 7: Leaf area index (LAI) of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] grown under irrigated (IRR) and rainfed conditions at Ukulinga during (b) 2010/11 and (a) 2011/12 planting seasons.

Leaf area index (LAI) was not consistent across seasons as was the case with plant height and leaf number. Results of LAI measured during 2010/11 showed highly significant differences ( $P < 0.001$ ) between irrigation treatments and landraces (Fig 7). Leaf area index was 70% lower under rainfed compared with irrigated conditions; the greatest reductions in LAI were observed in the KW landrace (Fig 7). Overall, the UM landrace was shown to have significantly higher LAI than the KW landrace. In the subsequent season (2011/12), results were consistent in that there were highly significant differences ( $P < 0.001$ ) between irrigation treatments. Based on mean values for irrigation treatments, LAI was 66% lower under rainfed compared to irrigated conditions. There were no significant differences between the landraces. However, the KW and UM landraces had higher LAI than the DL landrace under both irrigated and rainfed conditions. This was despite the fact that DL had larger-sized leaves (data not shown) than UM and KW. Overall, for both seasons, LAI was shown to be very sensitive to water stress as shown by the huge reductions in LAI under rainfed compared with irrigated conditions. The KW landrace was shown to have the greatest reductions in LAI under rainfed conditions compared with the UM landrace. The results of LAI observed in the KW landrace were consistent with decreased plant height and leaf number. Although the UM landrace showed a decreased plant height and leaf number, its reduction in leaf number were minimal; hence, it had better LAI under rainfed conditions.

The vegetative growth index (VGI) which considers all parameters related to vegetative growth (i.e. plant height, leaf number and area, suckers and stolons) was shown to be significantly lower under rainfed compared with irrigated conditions (Fig 8). Results for the VGI showed highly significant differences ( $P < 0.001$ ) between treatments and landraces. The interaction between irrigation treatments and landraces was also shown to be highly significant (Fig 8). Under rainfed conditions, VGI was 91% and 87% lower during the 2010/11 and 2011/12 planting seasons, respectively, relative to irrigated conditions. Decreases in VGI were highest in the KW and UM landraces (94% and 89%), respectively, compared with the DL landrace (86%). Reduction in VGI under rainfed conditions was consistent with results of reduced plant height, leaf number and leaf area index compared with irrigated conditions.



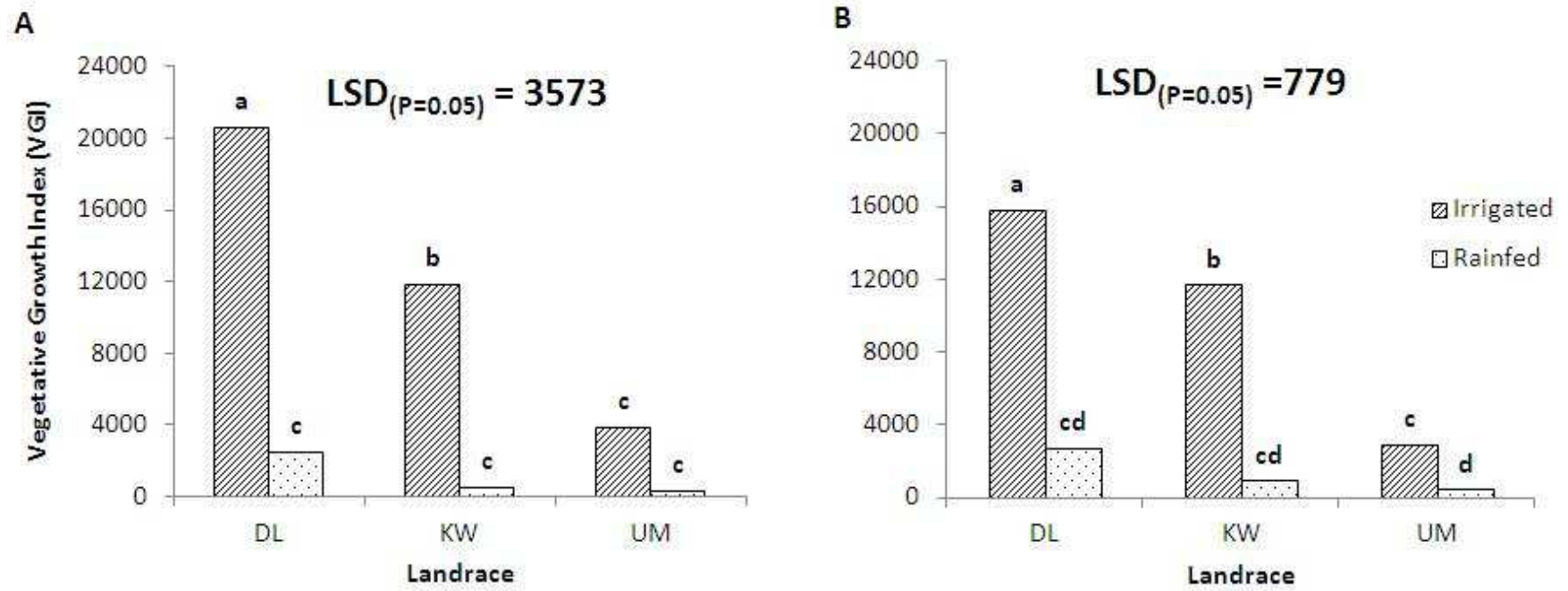


Figure 8: Vegetative growth index (VGI) of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] grown under irrigated and rainfed conditions at Ukulinga during A. 2010/11 and B. 2011/12 planting seasons.

## Crop phenology

Results of crop phenology, observed as time to harvest maturity, showed highly significant differences ( $P < 0.001$ ) between irrigation treatments as well as between landraces (Fig 9). Only the KW and UM landraces were evaluated for this parameter, because the DL landrace, a perennial, was not exhibiting any signs of harvest maturity. Time to harvest maturity decreased significantly under rainfed relative to irrigated conditions. Based on mean values, it took 32 weeks after planting (WAP) for taro to mature under irrigated conditions compared with 30 WAP under rainfed conditions. The UM landrace had a shorter crop duration under both irrigated and rainfed conditions compared with the KW landrace (Fig 9).

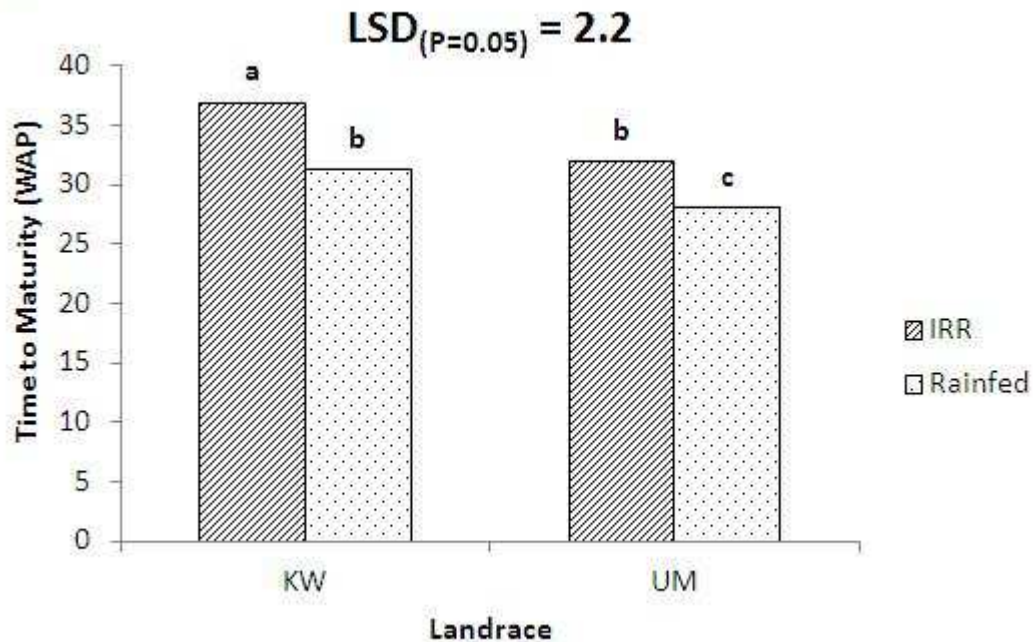


Figure 9: Time to harvest maturity, in weeks after planting, of taro landraces [KwaNgwanase (KW) & Umbumbulu (UM)] grown under irrigated (IRR) and rainfed conditions at Ukulinga during 2010/11 planting season. Note that DL is not included in this graph.

## Yield

The DL landrace failed to form yield across either season. This is most likely because the DL landrace is a non-domesticated perennial crop which normally grows in shallow rivers. As such our attempt to take it out of its natural habitat was unsuccessful. Results only show the KW and UM landraces (Tables 1 & 2). Due to differences in weather parameters between the two seasons, results presented here do not show the interaction between seasons. During the 2010/11 planting season, results of yield components and final yield were lower under rainfed relative to irrigated conditions (Table 1). Biomass, HI, corm number and corm mass were all lower under rainfed compared to irrigated conditions (Table 1). Results of biomass, corm mass and yield all showed highly significant differences ( $P < 0.001$ ) between irrigation treatments. Harvest index (HI) and corm number showed no significant differences between irrigation treatments (Table 1). Only biomass and HI showed significant differences between landraces (Table 1). Overall, yield ( $\text{t ha}^{-1}$ ) was higher under irrigated relative to rainfed conditions; yield was, on average, 65% lower under rainfed compared to irrigated conditions. The KW landrace had higher yield under irrigated conditions than the UM landrace only in 2010/11. This was consistent with the longer crop duration (Fig 9). The opposite was true under rainfed conditions, with the UM landraces having better yield than the KW landrace during both seasons. Under rainfed conditions, yield of the KW landrace was 75% lower compared with 52% in the UM landrace. The pattern of lower yield between the two landraces was consistent with trends in VGI; vegetative growth of the UM landraces was less affected by limited water availability under rainfed conditions (Fig 8). As such, lowering of final yield was mainly related to lower biomass per plant (Table 2). Correlation and path analysis of yield and yield determinants confirmed that biomass was highly correlated with yield ( $r = 0.9572$ ) and that biomass had the greatest direct contribution to yield (1.081931) (Table 2).

Table 1. Yield and yield components (biomass, harvest index, corm number and corm mass) of two taro landraces (KwaNgwanase (KW) and Umbumbulu (UM) grown under irrigated and rainfed conditions during 2010/11 and 2011/12 summer seasons. Numbers in the same column not sharing the same letter differ significantly at LSD (P = 0.05).

Season	Water Treatment	Landrace	Biomass	Harvest	Corm	Corm	Yield	
			plant <sup>-1</sup>	Index	number	mass		
			(kg)	(%)	plant <sup>-1</sup>	(kg)	(t ha <sup>-1</sup> )	
2010/11	IRRIGATED	Umbumbulu	1.03b	82.46a	13.72a	0.86b	17.14b	
		KwaNgwanase	1.95a	65.49b	20.56a	1.21a	24.16a	
	RAINFED	Umbumbulu	0.56b	74.23ab	12.14a	0.41c	8.26c	
		KwaNgwanase	0.52b	65.91b	13.11a	0.31c	6.13c	
	LSD (P=0.05) Water			0.36	8.34	7.47	0.19	3.76
	LSD (P=0.05) Landrace			0.36	8.34	7.47	0.19	3.76
	LSD (P=0.05) WT*Landrace			0.50	11.79	10.56	0.27	5.31
2011/12	IRRIGATED	Umbumbulu	1.32a	67.26a	14.97a	0.73a	14.63a	
		KwaNgwanase	0.89b	51.07a	7.29b	0.52ab	10.43ab	
	RAINFED	Umbumbulu	0.63bc	59.01a	15.19a	0.36b	7.27b	
		KwaNgwanase	0.49c	59.63a	8.11b	0.27b	5.39b	
	LSD (P=0.05) Water			0.20	21.61	4.82	0.25	5.01
	LSD (P=0.05) Landrace			0.20	21.61	4.82	0.25	5.01
	LSD (P=0.05) WT*Landrace			0.28	30.56	6.82	0.35	7.09

Table 2. Correlation matrix and path coefficients showing direct and indirect contributions of biomass, harvest index and corm number per plant to yield for both KwaNgwanase (KW) and Umbumbulu (UM) landraces during 2010/11 and 2011/12 planting seasons. Values in bold represent the direct contribution; <sup>i</sup> represents the indirect contribution and \* denotes the correlation coefficient.

Season		Harvest index	Corm number plant <sup>-1</sup>	Biomass	Correlation Coeff. Yield*
2010/1	1 Harvest index	<b>0.260343</b>	0.029004 <sup>i</sup>	-0.27925 <sup>i</sup>	0.0101
	1 Corm number plant <sup>-1</sup>	-0.09942 <sup>i</sup>	<b>-0.07595</b>	0.819671 <sup>i</sup>	0.6443
	1 Biomass	-0.06719 <sup>i</sup>	-0.05754 <sup>i</sup>	<b>1.081931</b>	0.9572
2011/1	2 Harvest index	<b>0.422679</b>	-0.02087 <sup>i</sup>	0.17119 <sup>i</sup>	0.573
	2 Corm number plant <sup>-1</sup>	0.088974 <sup>i</sup>	<b>-0.09914</b>	0.291366 <sup>i</sup>	0.2812
	2 Biomass	0.088509 <sup>i</sup>	-0.03533 <sup>i</sup>	<b>0.817524</b>	0.8707

During the subsequent season (2011/12), the trend was similar, with respect to differences between water treatments (Table 1). Yield components and final yield decreased under rainfed compared with irrigated conditions (Table 1). Yield in the irrigated treatment during 2011/12 was comparatively lower than that observed during 2010/11. Contrary to results from the first season, the UM landrace had higher biomass and yield than the KW landrace under both irrigated and rainfed conditions during the second season. Secondly, based on percentage yield decline under rainfed conditions, the UM landrace was shown to have performed better than the KW landrace under rainfed conditions (Table 1). Correlation and path analysis of yield and yield determinants for the second season were consistent with results of the first season (Table 2). Biomass was highly correlated to final yield ( $r = 0.8707$ ) and contributed highly (0.817524) towards final yield. The contribution of HI to final yield was minimal while corm number had the least contribution (Table 2). Corm number generally was not much lower under rainfed relative to irrigated conditions. This suggested that while corm number may be relatively consistent, individual corm size and mass decreased in response to limited water availability. Since biomass was shown to contribute most to yield, the UM landrace may be more suited to rainfed production due to a higher biomass (and consequently yield) under rainfed relative to irrigated conditions (Table 1).

## DISCUSSION

The findings of this study showed that taro landraces took at least 7 weeks to emerge. The KwaNgwanase (KW) (dasheen) and Umbumbulu (UM) (eddoe) landraces were better than the Dumbe Lomfula (DL) (wild unclassified) landrace. It should be noted that DL is a wild landrace naturally adapted to wetlands; hence this may have affected its performance. Slow emergence of taro landraces would imply that a lot of water is lost to soil evaporation during the establishment stage. Mare (2010) reported even longer establishment periods ( $\approx 10$  weeks) for several eddoe type landraces. Time taken to emerge may be reflective of different propagules used for each of the three landraces. KwaNgwanase was propagated using head-sets (huli), Umbumbulu and DL using sprouted corms and cuttings, respectively. This may have resulted in propagule type and size effects (Singh et al., 1998; Lebot, 2009); thus explaining differences observed between landraces.

Levitt (1972) is credited with categorising the different plant strategies to drought tolerance as escape, avoidance and tolerance. Stomatal closure, a drought avoidance mechanism (Levitt, 1979; Turner, 1986), is one of crops' initial responses to drought stress. The strategy is to minimise transpirational water losses (Chaves et al., 2003). It is widely accepted as the major limitation to photosynthesis and biomass production under drought stress (Chaves et al., 2002, 2003). Our findings showed that stomatal conductance decreased under rainfed compared with irrigated conditions. This was indicative of stomatal regulation. Under rainfed conditions, the UM landrace had the greatest decreases in stomatal conductance, indicating greater control of stomatal aperture than the KW and DL landraces. Sivan (1995) reported similar findings of decreasing stomatal conductance under water stress in two dasheen and eddoe taro varieties. Stomatal regulation may play a role in stress acclimation of taro landraces to water stress, specifically the UM landrace.

Under non-limiting conditions, plants ( $C_3$  plants in particular) utilise a large proportion of absorbed solar radiation for photosynthesis and photorespiration (Maroco et al., 1998). However, under conditions of limited water availability, plants have to find ways of getting rid of excess radiation. Loss of chlorophyll is one such strategy (Havaux and Tardy, 1999). The strategy is to effect a down-regulation of photosynthesis in response to decreased availability of intracellular  $CO_2$  resulting from stomatal closure. In this study it was shown that

chlorophyll content index decreased under rainfed relative to irrigated conditions, in line with decreasing stomatal conductance. This was evidence of energy dissipation mechanism in taro landraces. Our findings concur with Sahoo et al. (2006) who reported decreased chlorophyll stability index in a taro hybrid subjected to water stress. This response was clear in the UM landrace, suggesting the UM landrace was able to down-regulate its photosynthesis in line with decreasing CO<sub>2</sub> availability.

Plants also cope with limited water availability through reductions in plant size and surface area available for transpiration (Mitchell et al., 1998) as a drought avoidance strategy (Levitt, 1979; Turner, 1986). This study has shown that plant height, leaf number, LAI and VGI of landraces were lower under rainfed relative to irrigated conditions. Our findings were consistent with findings by Sahoo et al. (2006) that water stress decreased plant height, leaf number and leaf area of a taro hybrid. According to Lebot (2009), VGI is a unique taro specific index in that it considers all aspects of taro morphology – leaf number and area, plant height as well as suckers and stolons. It has been reported to be positively correlated to corm yield (Lebot, 2009). Our findings showed that VGI decreased under limited water availability compared with irrigated conditions. This was more pronounced during the 2011/12 season which was classified as a drought season. The reduction in VGI was due to failure by landraces to form suckers, coupled with reduced plant height, leaf number and leaf area under rainfed conditions. Over-all, the KW landrace was shown to be most sensitive to water stress compared to the UM and DL landraces. The UM landrace showed moderate decreases in vegetative components under stress suggesting that it was able to strike a balance between minimising water losses through transpiration while allowing for biomass production to continue. This was consistent with UM's degree of stomatal control and accompanying lowering of CCI.

Another plant strategy for coping with limited water availability is escape (Levitt, 1979; Turner, 1986). Plants that escape drought generally exhibit a degree of phenological plasticity through completing their life cycle before water stress becomes terminal. In this regard, taro landraces, especially the UM landrace, showed a degree of phenological plasticity in response to limited water availability under rainfed conditions. The UM landrace matured earlier under rainfed relative to irrigated conditions. This was consistent with decreased

vegetative growth under rainfed conditions. Rainfed conditions resulted in enhanced leaf shedding (reduced leaf number) which resulted in shortened crop duration. Blum (2005) associated drought avoidance with reduced season duration due to reduced leaf number. While reduction in leaf number is a drought avoidance mechanism, phenological plasticity is an escape mechanism. This agrees with Ludlow (1989) who suggested that drought tolerance strategies do not necessarily work in isolation.

Our findings on yield response to limited water availability were consistent with results of crop growth. Yield components and final yield were all lower under rainfed conditions relative to irrigated conditions. This concurs with Blum (2005) that plant drought responses that favoured avoidance and escape were often to the detriment of yield due to reduced crop duration and biomass production. Rainfed production resulted in yield losses of at least 50%, on average, in the KW and UM landraces while the DL landrace failed to form yield under both irrigated and rainfed conditions. It is worth noting that the DL landrace was obtained from the wild where it grows as a perennial. Our objective was to evaluate if it could be domesticated as an annual crop as has been done with the KW and UM landraces over a long period of time.

According to Farooq et al. (2009), many yield-determining plant processes are affected by water stress. Findings of the current study showed that the greatest contributor to yield attainment was biomass. However, biomass production was affected by reduced stomatal conductance and chlorophyll content, reduced vegetative growth and crop duration under rainfed conditions. Therefore, management practices that favour biomass production should be considered in order to maximise yield under conditions of limited water availability. The UM landrace which consistently produced relatively higher biomass under rainfed conditions may be suited for rainfed conditions where water is the primary limitation to crop production.



## **CONCLUSION**

This study showed that taro landraces were susceptible to drought stress under rainfed conditions. Attempts to domesticate the DL out of its native habitat were unsuccessful as the crop failed to produce yield. Future studies, which may include breeders, should evaluate whether there are any useful traits in the DL landrace that could be useful to future crop improvement. Nonetheless, the study managed to index drought strategies in taro landraces. Drought adaptation in taro landraces involved a combination of drought avoidance and escape mechanisms. Drought avoidance was achieved through stomatal regulation, energy dissipation and reduced canopy size. These responses had the net effect of reducing crop water losses to transpiration. Escape was demonstrated through phenological plasticity such that under water limited conditions, taro matured earlier. The KW landrace is more suited to irrigated conditions and therefore should be cultivated where supplementary irrigation is available. The UM landrace showed greater adaptability to water stress under rainfed conditions. As such, the UM landrace may be suited for rainfed production given that management practices that favour biomass accumulation are practised.

## **ACKNOWLEDGEMENTS**

Water Research Commission of South Africa K5/177/4 Water-Use of Drought Tolerant Crops. WRC Knowledge Review 2008-09.

## **References**

**(See final reference list pages 198-228)**

## CHAPTER 4

### **Response of taro (*Colocasia esculenta* L. Schott) landraces to varying water regimes under a rainshelter**

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## ABSTRACT

Taro [*Colocasia esculenta* (L.) Schott] is an underutilised crop in sub-Saharan Africa. There is no information describing water-use and drought tolerance of local taro landraces. Therefore, the objective of this study was to evaluate growth, yield and water-use of three South African landraces of taro under varying water regimes. Three taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) and Umbumbulu (UM)] were planted in a rainshelter (14, October, 2010 and 8, September, 2011) at Roodeplaat, Pretoria, South Africa. Three levels of irrigation [30%, 60% and 100% crop water requirement (ETa)] were applied three times a week using drip irrigation. Emergence, plant height, leaf number, leaf area index (LAI) and stomatal conductance were measured *in situ*. Root length, fresh and dry mass were obtained by destructive sampling. Yield, yield components and water-use efficiency were determined at harvest. Taro landraces showed slow and uneven emergence. Stomatal conductance was respectively 4% and 23% lower at 60% and 30% ETa relative to 100% ETa. Such a decline was clearer in the UM landrace, suggesting greater stomatal regulation in the UM landrace compared to KW and DL landraces. Plant growth parameters (plant height, leaf number and LAI) were lower by between 5 – 19% at 60% and 30% ETa, respectively, ETa relative to 100% ETa. The KW and DL landraces had very low growth while the UM landrace had moderate growth. Taro yield was 15% and 46% higher at optimum irrigation relative to 60% ETa and 30% ETa. Water-use efficiency was relatively unchanged (0.22 – 0.24 kg m<sup>-3</sup>) across varying water regimes. On average, the UM landrace had 113% higher WUE than the KW landrace. These findings can be used to differentiate the landraces on the basis of potential drought tolerance.

*Keywords:* Drought; Neglected underutilised species; Water-use efficiency; Yield

## 1. Introduction

Taro (*Colocasia esculenta* L. Schott) is a major root crop of the Araceae family with wide distribution in the tropics and subtropics (Lebot, 2009). It is among the oldest crops known to man with a history dating back to more than 10 000 years (Rao et al., 2010). However, the crop remains underutilised in much of the world, including South Africa, due to lack of information. The widely held perception that taro is one of the least water efficient crops (Uyeda et al., 2011) may, in part, explain its current low levels of utilisation. It therefore comes as no surprise that information describing water-use of taro and possible drought tolerance is scarce. Only recently has a major project been commissioned where one of the objectives is to breed for drought tolerance in taro (International Network of Edible Aroids (INEA) <http://www.ediblearoids.org>).

There were few reports in the literature describing drought tolerance of taro and its water-use (Sivan, 1995; Sahoo et al., 2006; Uyeda et al., 2011). Sivan (1995) studied drought tolerance in two dasheen and eddoe taro varieties, as well as tannia (*Xanthosoma sagittifolium*) and observed that stomatal conductance, leaf number and leaf area of both cultivars all decreased in response to water stress. In a separate study, Sahoo et al. (2006) subjected a taro hybrid to water stress using polyethylene glycol (PEG) and observed significant differences in plant growth parameters of height, leaf number and area as well as minimum yield reduction in response to water stress. Elsewhere, Uyeda et al. (2011) evaluated the response of three commercial taro varieties to five irrigation rates based on reference evapotranspiration ( $ET_0$ ) and found that irrigating taro at 150% of  $ET_0$  could maximise yield. Sahoo et al. (2006) went on to conclude that development of drought tolerant taro cultivars was possible while Uyeda et al. (2011) stated that upland taro varieties may be adapted to water-limited production. Therefore, evaluating responses of previously unstudied taro landraces to water stress may aid in identifying genotypes with drought tolerance and suitability for production in water-limited areas.

South Africa is classified as hyper-arid to semi-arid (Bennie and Hensley, 2001); water availability remains a major limiting factor to crop production and threatens household food security. Climate change pundits suggest that water will become even scarcer (Petit et al., 1999; Hassan, 2006), further threatening crop production and food security. Taro production

has been mainly confined to the coastal areas of KwaZulu-Natal and Eastern Cape provinces (Shange, 2004) where farmers still rely on landraces for planting material. It is possible that, over hundreds of years of farmer and natural selection, these landraces may have acquired drought tolerance and evolved to be productive under conditions of limited water availability under upland cultivation. However, this assumption remains to be tested rigorously, as has been done for other established crops.

As such, there is a need to evaluate responses of local taro landraces to water stress and determine their water-use under varying water regimes. Such information would allow for promotion of taro in areas with limited rainfall, but with access to irrigation. Furthermore, if indeed certain landraces have adapted to low levels of water-use that would contribute towards local and international breeding efforts for drought tolerance in taro. It was hypothesised that taro landraces have evolved under natural selection to become suited to water-limited conditions. Therefore, the aim of this study was to evaluate the growth, yield and water-use efficiency of three taro landraces under varying water regimes.

## **2. Material and methods**

### *2.1 Plant material*

South African taro landraces were sourced from KwaNgwanase (KW) (27°1'S; 32°44'E) in northern KwaZulu-Natal (KZN) province, and Umbumbulu [UM and Dumbe Lomfula (DL): 29°36'S; 30°25'E] situated in the midlands of KZN. The KW and DL landraces were classified as dasheen types characterised by a large edible central corm with few side cormels (Shange, 2004). The UM landrace was classified as an eddoe type landrace characterised by a central corm and numerous side cormels which are the edible part (Lebot, 2009). Propagules were initially selected for uniform size (Singh et al., 1998) before being treated with a bactericide and fungicide (Sporekill<sup>®</sup>) to prevent rotting during sprouting. Propagules were then sprouted in vermiculite (30°C; 90% RH) for 21 days before being planted.

### *2.2 Site description*

Trials were planted under a rainshelter at Roodeplaat, Pretoria (25°60'S; 28°35'E), South Africa, over two summer seasons (14 October, 2010 to June, 2011 and 8 September, 2011 to

May, 2011). In both seasons, the duration of the experiments was eight months. The rainshelter is designed to stay open when there is no rainfall, but to close when a rainfall event occurs, thus excluding the effect of rainfall from the experiment. Soil in the rainshelter was classified as sandy clay loam (USDA taxonomic system). The Soil Water Characteristics Hydraulic Properties Calculator (<http://hydrolab.arsusda.gov/soilwater/Index.htm>) was used to calculate the amount of water available at field capacity (FC), permanent wilting point (PWP), and saturation (SAT), as well as the saturated hydraulic conductivity (Table 1). Daily weather parameters [maximum and minimum air temperature, relative humidity, solar radiation, wind speed, rainfall and reference evapotranspiration( $ET_o$ )] for the duration of the experiments were monitored and collected from an automatic weather station located within a 100 m radius from the rainshelter.

### *2.3 Experimental designs*

The experimental design was a factorial experiment with two factors: irrigation level and landrace type, replicated three times. The three irrigation levels were 30%, 60% and 100% of crop water requirement ( $ET_a$ ). There were three landraces: Dumbe Lomfula (DL), KwaNgwanase (KW) and Umbumbulu (UM). The experiment was laid out in a randomised complete block design; individual plot size in the rainshelter was 6 m<sup>2</sup>, with plant spacing of 0.6 m x 0.6 m.

### *2.4 Irrigation*

Irrigation in the rainshelter was delivered using drip irrigation. The irrigation system comprised a pump, filters, 3 solenoid valves (one for each irrigation level), 3 water meters, a control box, online drippers, 200 litre JOJO tank, main line, sub-main lines and laterals. The maximum allowable operating pressure of the system was 200 kPa, with an average discharge rate per dripper of 2 l/hour. Dripper line spacing was based on actual plant spacing (0.6 m x 0.6 m). In order to prevent seepage and lateral movement of water between plots, a double-folded black, 200 µm thick polyethylene sheet, was trenched at a depth of 1 m between plots.

Irrigation scheduling was based on reference evapotranspiration ( $ET_o$ ) and a crop factor ( $K_c$ ) (Allen et al., 1998). Reference evapotranspiration ( $ET_o$ ) values were obtained from an automatic weather station (AWS); the AWS calculates  $ET_o$  on a daily basis according to the FAO Penman–Monteith's method (Allen et al., 1998). Taro is about 7 months (210 days)

duration crop and authors differ on how these may be divided based on growth stages (Lebot, 2009). Crop coefficient ( $K_c$ ) values for taro were as described by Fares (2008) whereby  $K_{c_{initial}} = 1.05$  (2 months),  $K_{c_{med}} = 1.15$  (4 months) and  $K_{c_{late}} = 1.1$  (1 month). Using these values of  $K_c$  and  $ET_o$  from the AWS, crop water requirement ( $ETa$ ) was then calculated as follows as described by Allen et al. (1998);

$$ETa = ET_o * K_c \quad \text{Equation 1}$$

Where  $ETa$  = crop water requirement

$ET_o$  = reference evapotranspiration, and

$K_c$  = crop factor

Initially, at the beginning of the study, all treatments were irrigated to field capacity (Table 1). Thereafter, the treatments were imposed. Irrigation was applied three times every week. Irrigation was applied during the mornings to ensure water availability during peak periods of demand in the day. The total actual amount of irrigation water applied, taking into consideration the initial watering, ranged from 1 288 mm (100%  $ETa$ ) to 1 009 mm and 800 mm for 60% and 100%  $ETa$ , respectively. The soil water status during the growing period was monitored using Theta probes (Fig 1).

**Table 1.** Soil physical properties of soil in the rainshelter. <sup>v</sup>PWP – permanent wilting point; <sup>w</sup>FC – field capacity; <sup>x</sup>SAT – saturation; <sup>y</sup>TAW – total available water; <sup>z</sup>Ksat – saturated hydraulic conductivity.

	<sup>v</sup> PWP	<sup>w</sup> FC	<sup>x</sup> SAT	<sup>y</sup> TAW	<sup>z</sup> Ksat
Textural class	———— vol % ————			(mm m <sup>-1</sup> )	(mm day <sup>-1</sup> )
Sandy clay loam	16.1	24.1	42.1	80	324.2

## 2.5 Agronomic practices

Soil samples were taken from the rainshelter prior to planting and submitted for soil fertility and texture analyses. Based on soil fertility results, an organic fertiliser (Table 2), Gromor Accelerator® (30 g kg<sup>-1</sup> N, 15 g kg<sup>-1</sup> P and 15 g kg<sup>-1</sup> K) was applied at a rate of 5 330 kg ha<sup>-1</sup> (Mare, 2010), with half being applied at planting and the balance applied 20 weeks after emergence. Routine weeding and ridging inside the plots were done by hand. Agronomic practices were similar for both planting seasons.

**Table 2.** Chemical properties of soil in the rainshelter.

Fe	Mn	Cu	Zn	K	Ca	Mg	Na	P	pH (H <sub>2</sub> O)	Org. C	Total N
-----mg kg <sup>-1</sup> -----									Water	-----%----	
7.09	120.56	3.50	19.56	165.86	804.26	262.57	27.65	41.44	7.89	0.73	0.048

## 2.6 Data collection

Soil water content in the plots was monitored using ML-2x Theta Probes connected to a DL-2 data logger (Delta-T Devices, UK). In each plot, two probes were carefully inserted within the root zone at an angle (< 90°) at depths of 30 cm and 60 cm, respectively, and then buried with soil. Data collection for SWC using the Theta probes was done every 4 hours.

Parameters determined during the course of the experiments were emergence [up to 49 days after planting (DAP)]. Thereafter, plant height, leaf number, leaf area index (LAI) and stomatal conductance (SC) were determined up to 30 weeks after planting (WAP). Plant height was measured from the base of the plant up to the base of the 2<sup>nd</sup> youngest fully unfolded leaf. Leaf number was counted only for fully unfolded leaves with at least 50% green leaf area. Leaf area index was measured using the LAI2200 Canopy Analyser (Li-Cor, USA & Canada) by taking one measurement above the canopy and four below canopy readings taken in a diagonal (1 m) in each plot using a 270° view cap. Stomatal conductance was measured between 10 am and midday using a steady state leaf porometer (Model SC-1, Decagon Devices, USA); measurements were taken on the abaxial leaf surface of the 2<sup>nd</sup> youngest fully unfolded leaf (Sivan, 1995). Upon termination of the experiments, biomass (B), harvest index



(HI) and corm yield (Y) were determined. Biomass was measured as the whole plant mass (shoot, corms and roots), corm yield was measured as the mass of edible corms; HI was then calculated as the proportion of Y to B. Stomatal conductance was only determined in 2011/12.

Plant samples were randomly taken from the non-experimental plants in each plot at four, five and six months after planting for determination of biomass accumulation and root length. Plants were carefully dug out to avoid damaging roots and thereafter root length was determined by measuring from the base of the plant to the tip of the longest root.

**Water-use efficiency (WUE):** water-use efficiency was determined as follows:

$$\text{WUE} = \text{Biomass} / \text{ETa} \quad \text{Equation 2}$$

Where: WUE = water-use efficiency in  $\text{kg m}^{-3}$ ,

Biomass = above ground biomass plus below ground portion in kg, and

ETa = crop evapotranspiration/ water-use/ crop water requirement in  $\text{m}^3$ .

### *2.7 Data analysis*

Analysis of variance (ANOVA) was used to statistically analyse data using GenStat® (Version 14, VSN International, UK). Least significant difference (LSD) was used to separate means at the 5% level of significance.

### 3. Results

#### 3.1 Meteorological conditions and soil water content

Table 3 summarises the weather conditions that prevailed during the growing season months (September to May). The two seasons' weather patterns were similar to longterm weather characteristics for Roodeplaat (Section 2.2), where the experimental site was located. Temperatures were cooler in April and May, which represents the onset of winter. These two months were also characterised by low wind speed, solar radiation and total reference evapotranspiration ( $ET_o$ ). Warmer temperatures (December to March) coincided with rapid vegetative growth stages of taro (Figs 3 and 4). This period was characterised by, high solar radiation and  $ET_o$ . Hence, the conditions were optimum for growth of taro. Figure 1 shows the soil water content measurements from the three water regimes. The measurements confirmed that there were indeed differences between the three water regimes.

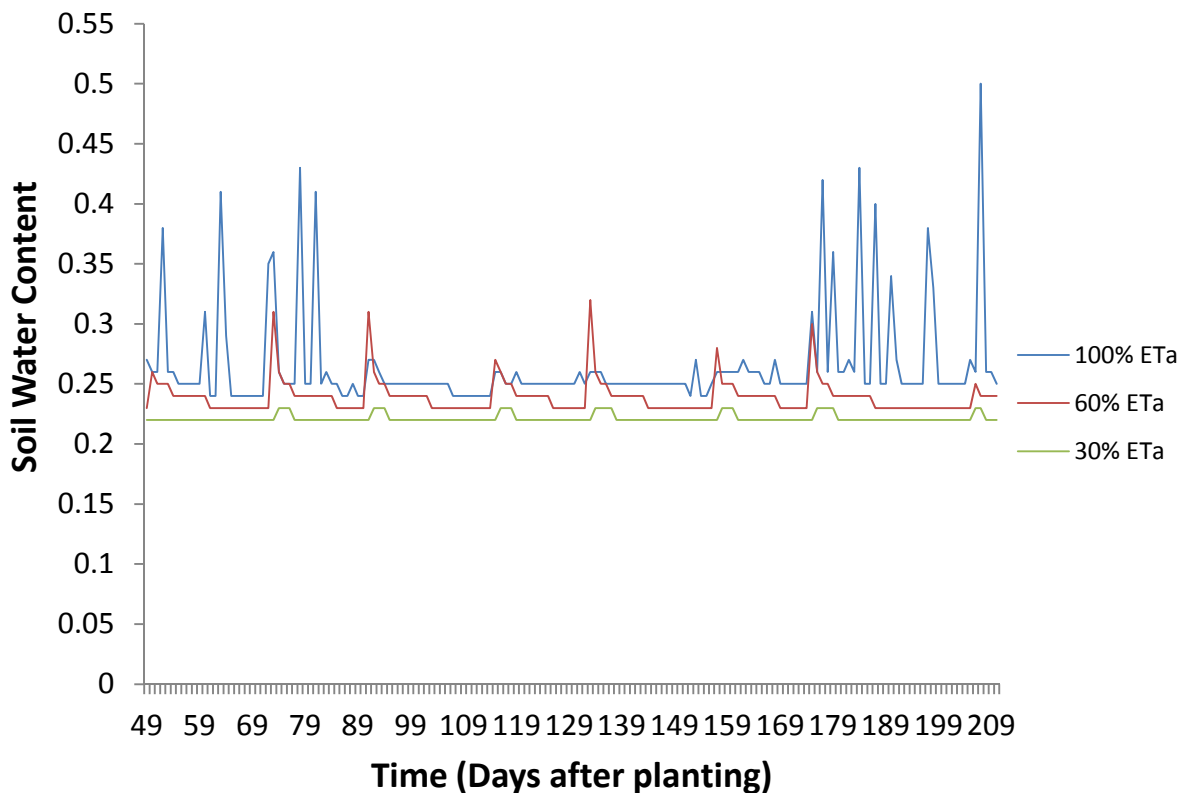


Figure 1: Volumetric soil water content observed in the rainshelter from 49 DAP showing differences between the 30%, 60% and 100% ETa water regimes.

**Table 3.** Summary of monthly averages for meteorological variables during the taro growing seasons.

<b>Season</b>					
<b>Month</b>	<b><sup>a</sup>T<sub>x</sub> (°C)</b>	<b><sup>b</sup>T<sub>n</sub> (°C)</b>	<b>Wind speed (m s<sup>-1</sup>)</b>	<b>Total radiation (MJ m<sup>-2</sup> day<sup>-1</sup>)</b>	<b><sup>c</sup>ET<sub>o</sub>* </b>
<b>2010-11</b>					
September	29.61	8.89	1.08	22.58	140.12
October	31.59	13.58	1.22	25.86	171.36
November	29.79	15.73	1.07	23.64	148.63
December	29.11	16.25	0.95	24.31	152.61
January	28.25	17.25	0.69	21.73	134.92
February	29.40	15.84	0.57	24.47	136.55
March	30.08	14.97	0.47	22.62	136.03
April	24.52	11.77	0.48	15.28	85.85
May	23.77	6.3	0.47	15.43	84.31
<b>2011-12</b>					
September	28.86	8.2	1.09	24.26	146.59
October	29.49	11.92	0.99	25.84	161.56
November	30.31	14.46	1.12	26.93	169.54
December	28.91	16.51	0.73	23.45	147.79
January	30.67	16.78	0.92	25.59	169.37
February	31.23	17.07	0.54	24.51	130.1
March	29.94	14.12	0.78	22.94	145.51
April	26.26	8.88	0.66	21.28	118.42
May	26.23	6.09	0.46	18.53	103.83

<sup>a</sup>Maximum temperature; <sup>b</sup>Minimum temperature; <sup>c</sup>FAO reference evapotranspiration;

\*Monthly total. Monthly averages and totals were calculated from hourly data. Note: meteorological variables do not include rainfall, because it was excluded in the rainshelter.

### 3.2 Crop establishment

Results of crop emergence showed differences between varieties (Fig 2). Irrigation treatment effects are not reported because all landraces were established under optimum 100% ETa treatment. Landraces were slow to emerge showing no uniformity (Fig 2), with zero emergence observed during the first 4 weeks after planting (WAP). There were highly significant differences ( $P < 0.001$ ) between landraces' emergence. The interaction between landraces and time (WAP) was also highly significant ( $P < 0.001$ ). The KW landrace was shown to emerge better (44.44%), with regards to emergence rate and uniformity, compared with the UM (38.89%) and DL (20.37%) landraces; DL had the lowest emergence rate over the time period observed.

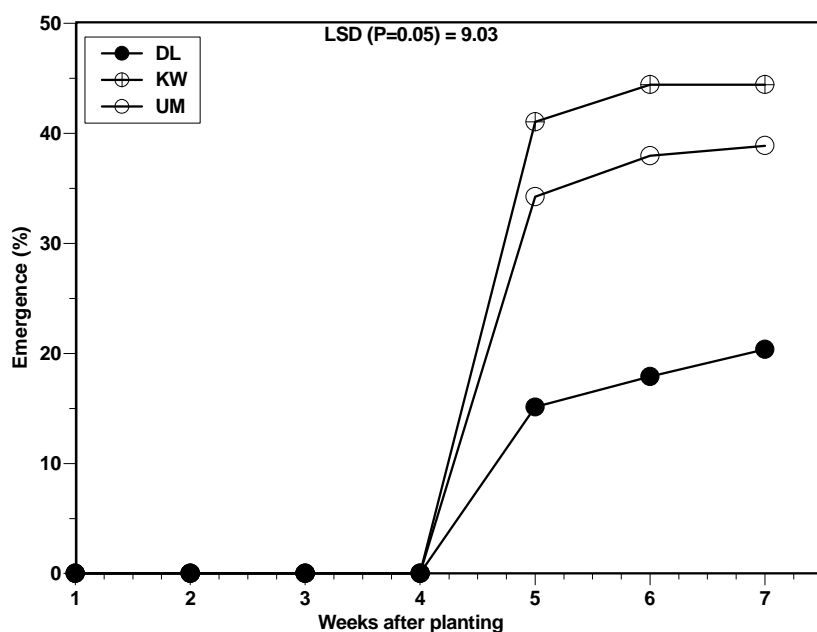


Figure 2: Emergence of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] based on mean values for both seasons (2010/11 and 2011/12).

### 3.3 Stomatal conductance

Stomatal conductance was significantly affected ( $P < 0.001$ ) by irrigation treatments (Fig 3). It was lower by about 4% and 23% at 60% and 30% ETa than at 100% ETa treatment. There were significant differences ( $P < 0.05$ ) between landraces; KW ( $204.6 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) and DL ( $204.4 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) landraces were similar while stomatal conductance of the UM landrace was 19% lower than the two landraces. The interaction between irrigation treatments and landraces was significant ( $P < 0.05$ ). Stomatal conductance of the DL and KW landraces was between 3-30% higher at 60% ETa compared to 100% and 30% ETa. Stomatal conductance of the UM landrace was lower by 25% and 40% at 60% ETa and 30% ETa than at 100% ETa. In addition, stomatal conductance of the UM landrace was 25% and 32% lower than the KW and DL landraces, respectively, at 30% ETa. Stomatal conductance of the DL and KW landraces, measured at 30% ETa, was respectively 6% and 15% higher than stomatal conductance of the UM landrace at 60% ETa. Overall, results of stomatal conductance pointed to the UM landrace having greater stomatal regulation, in response to decreasing water availability, than the KW and DL landraces.

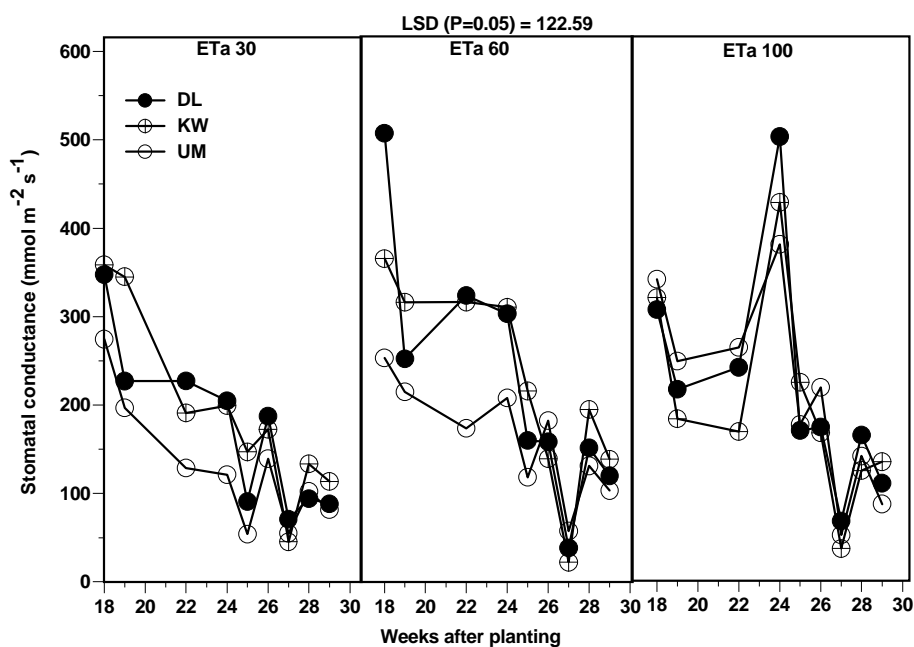


Figure 3: Stomatal conductance of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] in response to three levels of irrigation (30%, 60% and 100% ETa) during 2010/11 and 2011/12 seasons.

### 3.4 Crop growth

Plant height showed highly significant differences ( $P < 0.001$ ) between irrigation treatments (Fig 4). Plant height was 15% and 19% lower at 60% ETa and 30% ETa than at 100% ETa. There were also highly significant differences ( $P < 0.001$ ) between landraces; the trend was DL > KW > UM during 2010/11 season and DL > UM > KW during 2011/12. The DL landrace was the tallest at 100% ETa at the end of the season while the KW landrace showed the greatest reduction ( $\approx 15\%$ ) in plant height (after 16 weeks) in response to decreasing water availability at 60% and 30% ETa, respectively. The UM landrace showed moderate reduction ( $\approx 7\%$ ) in plant height under conditions of decreasing water availability.

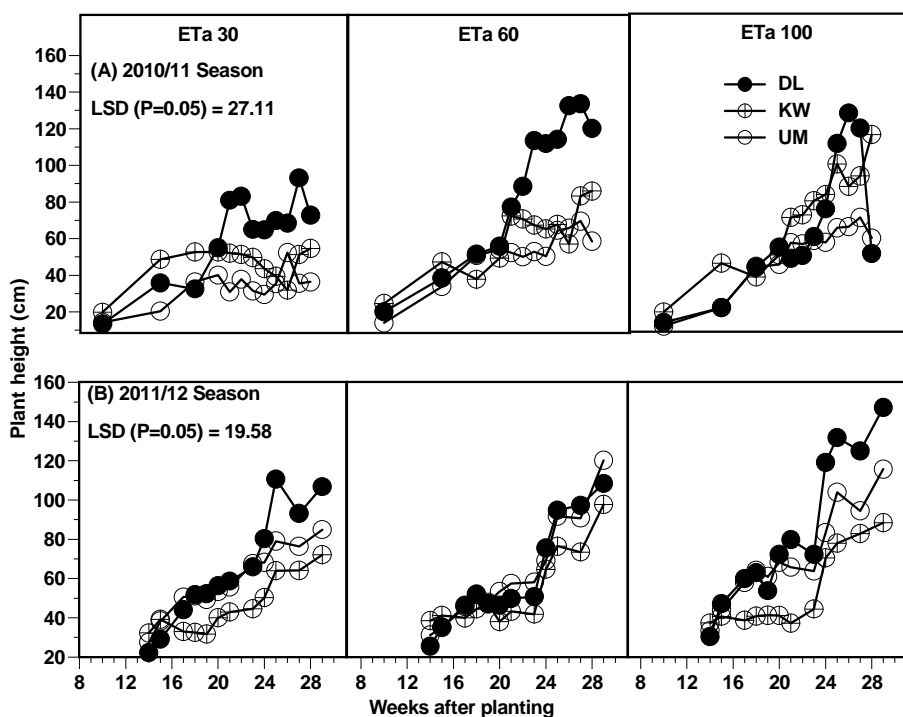


Figure 4: Plant height (cm) of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] in response to three levels of irrigation (30%, 60% and 100% ETa) during 2010/11 and 2011/12 seasons.

Leaf number followed the same trend as plant height. Highly significant differences ( $P < 0.001$ ) were shown between irrigation treatments as well as between landraces, with respect to leaf number (Fig 5). During 2010/11, the trend observed for leaf number was 100% ETa > 60% ETa > 30% ETa; however, during 2011/12 the trend was 60% ETa > 100% ETa > 30% ETa. Mean separation showed that leaf number at 100% ETa was statistically similar to 60% ETa but significantly less by 6% at 30% ETa. Thus, irrigation at 30% ETa consistently resulted in plants with the least number of leaves. With respect to differences observed between landraces, the trend was such that UM > DL > KW, while in 2011/12 the trend showed that KW > UM > DL. Similar to plant height, the KW landrace showed the greatest reduction ( $\approx 5\%$ ) in leaf number in response to limited water availability at 30% ETa. As with plant height, the UM landrace showed moderate reduction in leaf number in response to decreasing water availability.

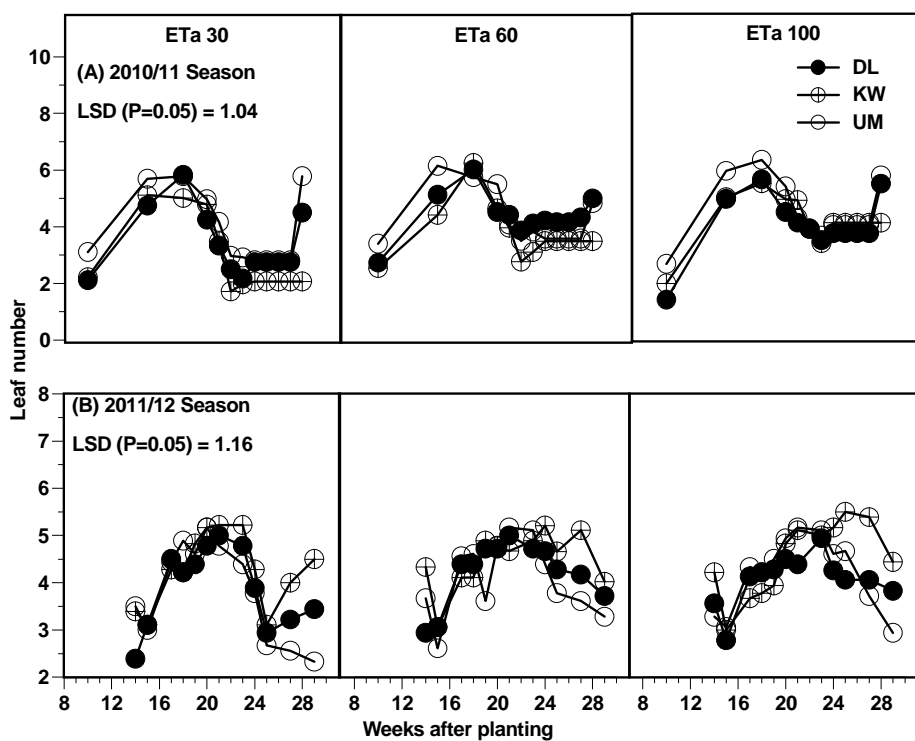


Figure 5: Leaf number of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] in response to three levels of irrigation (30%, 60% and 100% ETa) during 2010/11 and 2011/12 seasons.

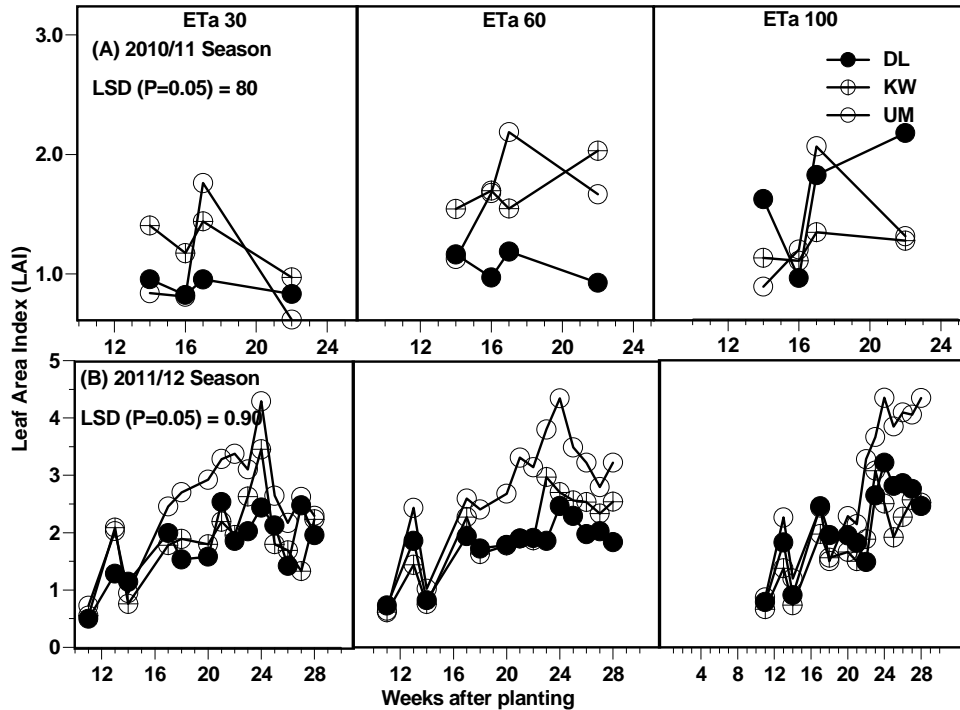


Figure 6: Leaf area index (LAI) of taro landraces [Dumbe Lomfula (DL), KwaNngwanase (KW) & Umbumbulu (UM)] in response to three levels of irrigation (30%, 60% and 100% ETa) during 2010/11 and 2011/12 seasons.

Leaf area index (LAI), which represents the whole canopy size, was shown to be significantly ( $P < 0.001$ ) affected by water availability (Fig 6). This was clearer during the 2011/12 season, possibly due to an increased number of observations compared to 2010/11 season. Leaf area index was 5% and 12% lower at 60% ETa and 30% ETa than LAI at 100% ETa treatments. This was consistent with measurements of plant height and leaf number which showed much lower values at 30% ETa. There were highly significant differences ( $P < 0.001$ ) between landraces ( $UM > KW > DL$ ) during the 2011/12 season. There was a significant ( $P < 0.001$ ) interaction between the irrigation treatments and landraces. The UM landrace's LAI was shown to be similar at 100% and 60% ETa but it was statistically lower ( $\approx 14\%$ ) at 30% ETa. Consistent with observations on plant height and leaf number, lower water application resulted in lower LAI for all landraces; the extent of such reduction differed between landraces.



A fluctuating growth pattern was observed for plant height, leaf number and LAI (Figs 4, 5 and 6). This was possibly due to the nature of taro vegetative growth. Taro landraces continuously shed older leaves, replacing them with younger ones. As such, this distorts measurements of growth parameters (Section 2.6), resulting in the observed fluctuations.

### *3.5 Biomass and root length*

Destructive sampling was done for the 2011/12 season, at monthly intervals (5-7 months after planting), to determine plant fresh mass (FM), dry mass (DM), root length and the ratio between dry to fresh mass (DM:FM) (Fig 7 and 8). Results showed huge variability. Fresh mass was significantly ( $P < 0.05$ ) affected by irrigation treatments giving 15% and 37% lower values at 60% ETa and 30% ETa (Fig 7). Although there were no significant differences ( $P > 0.05$ ) between landraces, their interaction with irrigation treatments was shown to be significant. The UM landrace had 2% and 40% more fresh mass at 100% ETa than the DL and KW landraces, respectively; KW had 8% and 25% lower fresh mass than UM and DL at 30% ETa. Dry mass per plant showed no significant differences ( $P > 0.05$ ) between irrigation treatments. Results showed that DM was respectively 77% and 12% higher at 60% ETa relative to 100% and 30% ETa (Fig 7). The ratio between fresh and dry mass (FM:DM) showed the same trend as that observed for DM with respect to differences between irrigation treatments and landraces (Fig 8).

Plant root length was significantly ( $P < 0.05$ ) affected by irrigation treatment (Fig 8). Decreasing water application resulted in lower root length; landraces had 2% and 19% less root length at 60% ETa and to 30% than at 100% ETa. There were also highly significant differences ( $P < 0.001$ ) between landraces (DL > KW > UM) while the interaction of the two factors was also highly significant ( $P < 0.001$ ). On average the UM landrace had 3% and 24% shorter roots than the KW and DL landraces, respectively.

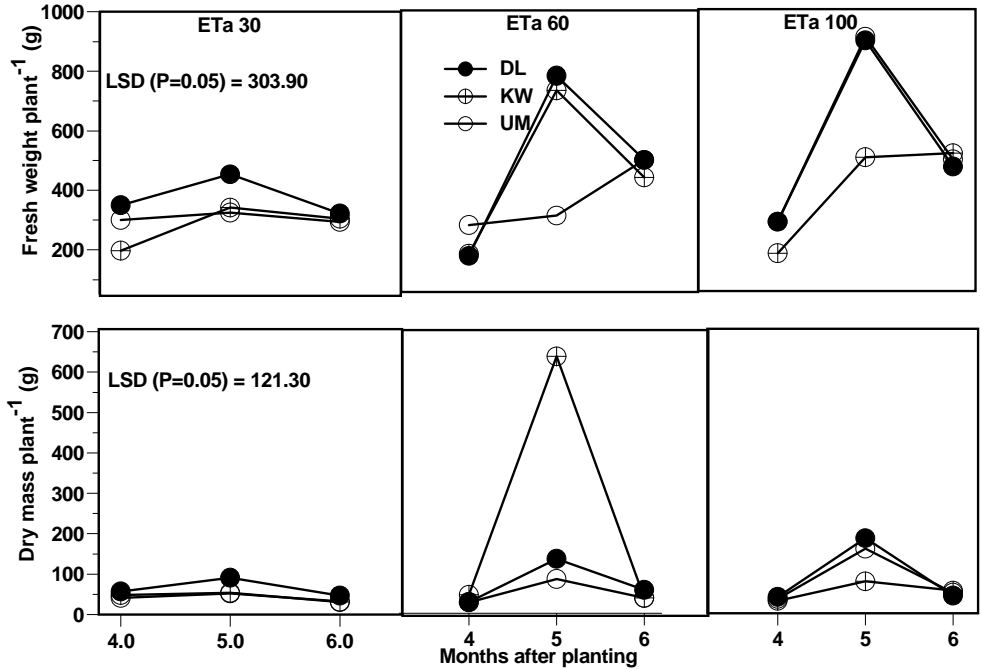


Figure 7: Fresh and dry mass ( $\text{g plant}^{-1}$ ) of taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] in response to three levels of irrigation (30%, 60% and 100% ETa) during 2010/11 and 2011/12 seasons.

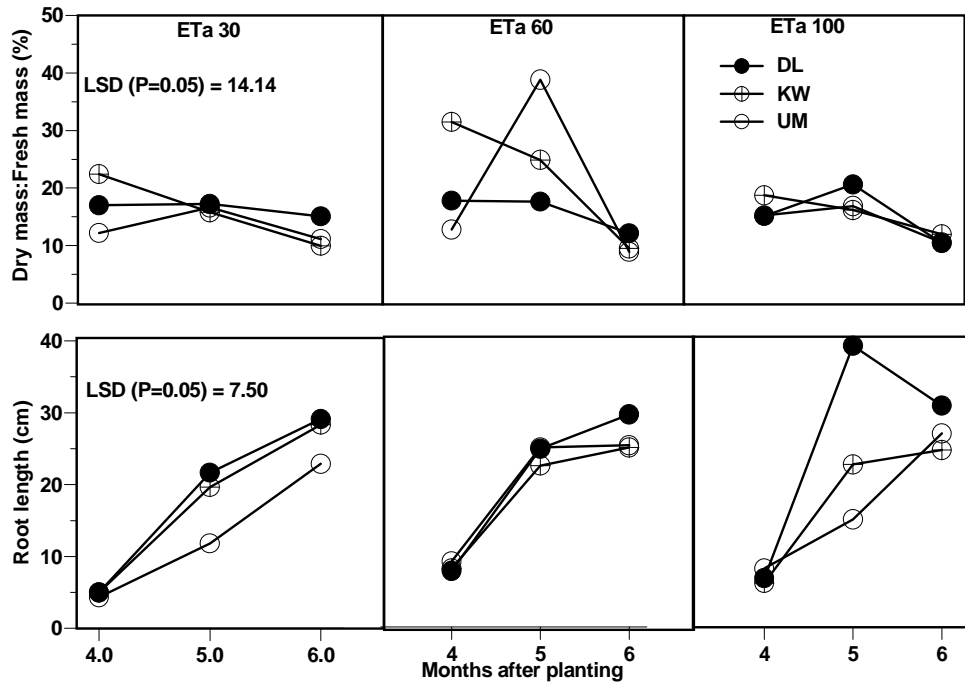


Figure 8: Root length (cm) and fresh: dry mass ratio (%) taro landraces [Dumbe Lomfula (DL), KwaNgwanase (KW) & Umbumbulu (UM)] in response to three levels of irrigation (30%, 60% and 100% ETa) during 2010/11 and 2011/12 seasons.

### *3.6 Yield and water-use*

Results of yield and yield components reported in this paper are only for the KW and UM landraces (Table 4). The DL landrace produced no yield, most likely because it is a wild landrace whose natural habitat is in shallow streams. Results of final biomass, for the two landraces, showed highly significant differences ( $P < 0.001$ ) between seasons (Table 4). Based on mean values for the seasons, final biomass during 2011/12 was at least 68% greater than that observed during 2010/11. Results of final biomass also showed significant differences ( $P < 0.05$ ) between irrigation treatments as well as between landraces. Final biomass was shown to be lower in response to decreasing water application rates (100% ETa > 60% ETa > 30% ETa). With regards to differences between landraces, the UM landrace had about 69% higher final biomass relative to the KW landrace under all three irrigation treatments. The trend in final biomass was consistent with results for plant growth, whereby the KW landrace was shown to be most affected by limited water availability.

Another key yield component was corm number per plant, especially for the UM landrace whereby the side cormels are consumed. The trend of results was similar to that observed for biomass. There were highly significant differences ( $P < 0.001$ ) between the two seasons, and significant differences ( $P < 0.05$ ) between irrigation treatments as well as between landraces (Table 4). On average, corm number per plant was 78% higher in 2011/12 than that in 2010/11. Interestingly, treatment means showed that corm number was respectively 13% and 11% higher at 60% ETa than at 100% and 30% ETa; this was also confirmed by mean separation using LSD ( $P = 0.05$ ) (Table 4). The UM landrace had about 92% higher corm number per plant than the KW landrace; this was due to morphological differences between the two landraces (Section 2.1).

**Table 4.** Yield and yield components (biomass, harvest index, corm number and corm mass) of two taro landraces (KwaNgwanase (KW) and Umbumbulu (UM) grown under a rainshelter at three irrigation levels (30, 60 and 100% ETa) during 2010/11 and 2011/12 summer seasons. \*Numbers in the same column not sharing the same letter differ significantly at LSD (P = 0.05).

Season		Corm					
Water Levels	Landrace	Biomass plant <sup>-1</sup> (kg)	Corm number plant <sup>-1</sup>	mass plant <sup>-1</sup> (kg)	Harvest Index (%)	Yield (t ha <sup>-1</sup> )	WUE (kg m <sup>-3</sup> )
<b>2010/11 Season</b>							
30% ETa	UM	0.248e	9.06c	0.220cd	87a	6.10cd	0.15c
	KW	0.183e	3.88e	0.156d	86a	4.32d	0.11c
60% ETa	UM	0.370de	8.11cd	0.336cd	90a	9.31cd	0.17c
	KW	0.164e	6.20cde	0.138d	86a	3.83d	0.07c
100% ETa	UM	0.377de	9.06c	0.324cd	85a	9.00cd	0.12c
	KW	0.227e	3.46e	0.152d	57c	4.23d	0.06c
<b>2011/12 Season</b>							
30% ETa	UM	0.886bc	16.56b	0.467bc	62bc	12.96ab	0.53a
	KW	0.288e	2.44e	0.205cd	71abc	5.70cd	0.17c
60% ETa	UM	1.086ab	22.56a	0.804a	74abc	22.32a	0.49a
	KW	0.478cde	3.28e	0.386bcd	82ab	10.70bcd	0.22c
100% ETa	UM	1.368a	21.78a	0.861a	63bc	23.90a	0.44ab
	KW	0.822bcd	4.28de	0.625ab	79ab	17.33ab	0.27bc
<b>LSD (P=0.05) Season</b>		0.179	1.53	0.102	8	2.82	0.08
<b>LSD<sub>(P=0.05)</sub> Water Treatment</b>		0.220	1.874	0.124	9	3.45	0.10
<b>LSD<sub>(P=0.05)</sub> Landrace</b>		0.179	1.53	0.102	8	2.82	0.08
<b>LSD<sub>(P=0.05)</sub> WT*Landrace</b>		0.311	2.65	0.176	13	4.88	0.14
<b>LSD<sub>(P=0.05)</sub></b>							0.20
<b>Ssn*WT*Landrace</b>		0.440	3.75	0.249	19	6.90	

Corm mass per plant also differed significantly ( $P < 0.001$ ) between seasons, being higher ( $\approx 150\%$ ) during 2011/12 compared with 2010/11. Irrigation treatments were also shown to have a significant effect on plant corm mass; based on treatment means alone, corm mass per plant was lower at lower water application rates ( $100\% \text{ ETa} > 60\% \text{ ETa} > 30\% \text{ ETa}$ ). Although corm number per plant was respectively 13% and 11% higher at 60% ETa compared with 100% and 30% ETa, this did not correlate with corm mass, suggesting that the numerous corms were small. The two landraces also differed significantly ( $P < 0.001$ ), with respect to corm mass (UM > KW). Mean separation using LSD ( $P = 0.05$ ) showed that corm mass of the UM landrace at 100% and 60% ETa were statistically similar, while corm mass was statistically less (44%) at 30% ETa. The general trend in corm mass showed much variation, although corm mass was less affected at 60% ETa (Table 4).

In line with observations on biomass, corm number and corm mass, harvest index (HI) showed significant differences ( $P < 0.05$ ) between the two seasons. Unlike other yield components, HI was 14% higher during 2010/11 compared with 2011/12. This was due to reduced vegetative growth and biomass (the denominator) during 2010/11. There were significant differences ( $P < 0.05$ ) between the three irrigation treatments only in 2011/12. Contrary to the trend observed for the other parameters, HI was respectively 14% and 7% lower at 100% ETa than at 60% and 30% ETa; mean separation confirmed this trend (Table 4). The fact that HI was higher under conditions of limited water availability implied a positive effect of stress on HI. Additionally, HI seemed to be more sensitive to changes in biomass than corm mass. There were no significant differences ( $P > 0.05$ ) between the landraces; based on mean values for landraces, they both had an average HI of 77%.

Consistent with results of yield components reported above, final yield ( $\text{t ha}^{-1}$ ) showed highly significant differences ( $P < 0.001$ ) between seasons. On average, yield was higher ( $\approx 150\%$ ) during 2011/12 compared to 2010/11 (Table 4). Irrigation treatments were shown to have a significant effect ( $P < 0.05$ ) on final yield, with yield being lower at lower water application rates ( $100\% \text{ ETa} > 60\% \text{ ETa} > 30\% \text{ ETa}$ ). The extent of yield reduction was greater at 30% ETa than at 60% ETa; based on mean values for irrigation treatments, yield was 15% and 47% lower at 60% ETa and 30% ETa than at 100% ETa. This re-affirmed the trend observed so far indicating that differences between 100% and 60% ETa were minimal,

while 30% ETa had the greatest effect on all parameters measured. With respect to differences between landraces, analysis of variance showed highly significant differences ( $P < 0.001$ ) between landraces, with the UM landrace out-yielding the KW landrace under all conditions. The performance of UM, especially under limited water availability, was consistent with the moderate reductions observed for growth parameters.

Water-use efficiency (WUE) also showed highly significant differences ( $P < 0.001$ ) between seasons, in line with the trend observed for yield components and final yield (Table 4). Interestingly, results showed that there were no significant differences ( $P > 0.05$ ) between the three irrigation treatments. A closer look at irrigation treatment means showed that, on average, WUE was slightly higher (9%) and similar at 30% and 60% ETa ( $0.24 \text{ kg m}^{-3}$ ) compared to 100% ETa ( $0.22 \text{ kg m}^{-3}$ ). Results also showed highly significant differences between landraces, with the UM landrace ( $0.32 \text{ kg m}^{-3}$ ) having higher (113%) WUE than the KW landrace ( $0.15 \text{ kg m}^{-3}$ ); mean separation also confirmed this.

### *3.7 Yield determinants in taro landraces*

Results of biomass, harvest index, corm number per plant (CMN) and WUE were subjected to correlation and path analysis to identify the parameter(s) that contributed most to final yield (Table 5). Biomass ( $r = 0.92$ ), CMN ( $r = 0.73$ ) and WUE ( $r = 0.67$ ) were shown to be highly correlated to final yield (Table 5). The parameter that had the greatest contribution to final yield was biomass, followed by harvest index (Table 5). Corm number had the least contribution to final yield, while WUE had a negative contribution to yield. The low contribution of corm number per plant relates to observations that high CMN did not translate to high yield (Table 4). This suggests that any selection effort should target a landrace with minimum biomass reduction under limited water availability.

**Table 5.** Correlation matrix and path coefficients showing direct and indirect contributions of biomass, harvest index and corm number per plant to yield for both KwaNgwanase (KW) and Umbumbulu (UM) landraces. <sup>x</sup> CMN = corm number per plant; <sup>y</sup> WUE = water-use efficiency. Values in bold represent the direct contribution; <sup>i</sup> represents the indirect contribution and \* denotes the correlation coefficient.

	<b>Biomass</b>	<b>Harvest index</b>	<sup>x</sup> <b>CMN</b>	<sup>y</sup> <b>WUE</b>	<b>Yield*</b>
<b>Biomass</b>	<b>1.21</b>	-0.18 <sup>i</sup>	0.06 <sup>i</sup>	-0.16 <sup>i</sup>	0.92
<b>Harvest index</b>	-0.65 <sup>i</sup>	<b>0.34</b>	-0.03 <sup>i</sup>	0.13 <sup>i</sup>	-0.22
<sup>x</sup> <b>CMN</b>	0.93 <sup>i</sup>	-0.14 <sup>i</sup>	<b>0.08</b>	-0.14 <sup>i</sup>	0.73
<sup>y</sup> <b>WUE</b>	1.03 <sup>i</sup>	-0.23 <sup>i</sup>	0.06 <sup>i</sup>	<b>-0.19</b>	0.67

#### 4. Discussion

Emergence of taro landraces was slow and erratic, with landraces failing to reach 50% emergence by 49 days after planting. Previously, Mare (2010) reported that it took about 70 days after planting for taro landraces to emerge under dryland conditions. Vigorous and uniform emergence is important for canopy cover (Passioura, 2006; Blum, 2012); thence the ability to quickly emerge (vigour) and start photosynthesising is important (Harris et al., 2002; Passioura, 2006). Good seedling establishment ensures rapid ground cover (Passioura, 2006) thereby reducing loss of water to soil evaporation. Slow emergence of taro landraces implies that a significant amount of water is lost to soil evaporation (unproductive) as opposed to being lost through transpiration during establishment (Blum, 2012). This would result in a significant amount of water being lost to evaporation in cases where the crop is irrigated using sprinkler or surface irrigation methods that have a high percentage of soil surface wetted. The use of drip irrigation, which has a smaller percentage wetted soil surface, would save water (Phene et al., 1994; Unlu et al., 2006).

A plant's ability to tolerate dry conditions is intricately linked to its ability to acclimatise (Anjum et al., 2011). Stomata facilitate water loss through transpiration as well as uptake of CO<sub>2</sub> from the atmosphere. In the current study, stomatal conductance was shown to decrease in response to decreasing water availability; this pattern was lucid for the UM landrace. Sivan

(1995) reported similar findings of declining stomatal conductance in taro varieties subjected to water stress. Under limited water availability, stomatal conductance decreases as a mechanism to minimise transpirational water losses (Chaves et al., 2003) – this is dehydration avoidance (Levitt, 1979; Turner, 1986). In this regard, it can be assumed that the UM landrace is the most water-efficient of the three landraces as evidenced by its greater degree of stomatal control.

Limited water availability has been reported to result in reduced plant growth due to impairment of cell division and expansion (Hussain et al., 2008). The trend observed showing lower canopy size (plant height, leaf number and LAI) under limited water availability (60% and 30% ETa) was consistent with reports by Sivan (1995) and Sahoo et al. (2006) who also observed reduced growth in taro varieties subjected to water stress. Reduction in leaf number was also due to premature senescence of leaves. Canopy size represents surface area available for transpiration; plants cope with reduced water availability through reductions in canopy size (Mitchell et al., 1998) – a dehydration avoidance mechanism (Levitt, 1979; Turner, 1986). In addition, reduced LAI has previously been ascribed to reduction in photosynthesis and assimilate supply under water limited conditions (Anjum et al., 2011) which curtail leaf expansion.

Reduction in canopy size in response to limited water availability is an attribute of water-use efficiency; however, this should not be excessive as leaf area directly correlates to biomass production and yield (Blum, 2005, 2012). Hypothetically, a plant that shows moderate reduction in canopy size is capable of striking a balance between minimising water loss and allowing for reasonable biomass production to continue. In this regard, the UM landrace was efficient in achieving both aspects - while the crop reduced its canopy size under limited water conditions, such reduction was moderate compared with the DL and KW landraces. This allowed the UM landrace to have higher biomass compared with the other landraces.

Under limited water availability, roots grow until demand for water is met. However, genetic variations may limit potential maximum rooting depth (Blum, 2005). A well-developed root system allows for enhanced capture of soil water (Passioura et al., 2006) an important adaptation (dehydration avoidance) to water limited conditions (Vurayai et al., 2011). This study showed that taro landraces had shallow roots (< 30 cm); this suggests that



taro landraces are unable to utilise water from deeper areas of the soil, a situation that may result in drainage losses (Passioura et al., 2006). Root length of taro landraces decreased with decreasing water availability. This was contrary to other studies that have reported increased root length under conditions of limited water availability – sunflower (Tahir et al., 2002) and *Populus sp* (Wullschleger et al., 2005). Moreover, this was also contrary to reports by Sivan (1995) of increased root: shoot in taro varieties subjected to water stress. We can only hypothesise that perhaps the constant re-wetting of the root zone, at all water levels, due to frequent irrigation by drip may have kept the root zone reasonably moist enough to discourage root growth.

Most plant adaptations associated with increased WUE under limited water availability are often detrimental to yield attainment, which is the goal of farming (Blum, 2005; Jaleel et al., 2009). Yield and yield components all decreased in response to reduced water availability. Despite the fact similar agronomic practices were done for both seasons, yield was significantly higher during 2011/12 compared with 2011/11. Differences in yield between seasons may be due to landrace variability. Yield decreased by 15% and 47% in response to reduced water availability at 60% ETa and 30% ETa, respectively, compared with the 100% ETa treatment. The trend was similar to recent reports on yield and water use efficiency of potato grown under different irrigation levels (Badr et al., 2012). They reported that tuber yield of potatoes decreased with decreasing amount of irrigation applied.

Water-use efficiency of taro landraces was shown to be constant across water regimes (0.22 - 0.24 kg m<sup>-3</sup>). The increase in WUE under limited water availability was marginal. Under limited water availability, WUE increases through either increasing yield (biomass) or decreasing water-use through the amount of irrigation applied (Pandey et al., 2000). Over-all, WUE of taro landraces was low compared to that reported for other crops such as potato (Badr et al., 2009). In the present study, decreasing the amount of irrigation applied, did not significantly improve WUE. This was shown in corresponding reductions in biomass and yield. Percentage yield reduction may have been equal to percentage reduction in water-use (water applied). On average, the UM landrace's WUE (0.32 kg m<sup>-3</sup>) was twice as high as that of the KW landrace (0.15 kg m<sup>-3</sup>). Uyeda et al. (2011) reported that upland taro was more efficient at using water than varieties which are more adapted to flooded conditions. The UM

landrace is an upland variety while the KW landrace is cultivated along the coast in swamps and other waterlogged areas.

Correlation and path analysis of taro yield determinants showed that biomass was highly correlated to yield and had the greatest contribution to yield. Corm number per plant had less contribution to final yield, suggesting that it is corm mass, not number, which is more critical under limited water availability. This partly explains why the UM landrace was able to out yield the KW landrace under all conditions. Yield reduction under limited water availability is a function of reduced canopy growth and biomass production (Badr et al., 2012). The UM landraces had moderate reductions in plant growth compared with the KW landrace and therefore, was able to produce more biomass which translated to higher yield. Yield of the UM landrace in the 30% ETa treatment during both seasons was higher than the global average yield estimate for taro ( $6.5 \text{ t ha}^{-1}$ ) (FAOSTAT, 2012).

## **5. Conclusion**

Given the importance of vigorous emergence, strategies to improve emergence of taro should be a key objective of future studies. This would improve water-use and possibly yield. Under conditions of limited water availability, taro landraces were able to reduce their water-use through reductions in stomatal conductance and canopy size. The extent of reduction in canopy size was greater in the KW landrace compared with the UM landrace suggesting that the KW landrace was more sensitive to limited water availability. The UM landrace was shown to have a greater degree of stomatal control, thus minimising water loss through transpiration. Yield was shown to decrease in response to limited water availability while WUE remained relatively unchanged across water treatments. The UM landrace was shown to have higher WUE and to be better adapted for cultivation in areas with limited water availability.

## **Acknowledgements**

Water Research Commission of South Africa K5/177/4 Water-Use of Drought Tolerant Crops. WRC Knowledge Review 2008-09.

## **References**

**(See final reference list pages 198-228)**

## CHAPTER 5

### **Growth, phenological and yield responses of a bambara groundnut (*Vigna subterranea* L. Verdc) landrace to imposed water stress: I. Field conditions**

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## **Abstract**

Bambara groundnut (*Vigna subterranea* L. Verdc) is an underutilised species with potential to contribute nutritional and food security in marginal areas. Growth, phenology and yield of a local bambara groundnut landrace from Jozini, KwaZulu-Natal, characterised into three selections according to seed coat colour, namely – Brown, Red and Light-brown – were evaluated under irrigated and rainfed field conditions at Roodeplaat, Pretoria. Replicated (x3) trials were planted under rainfed and irrigated conditions with seed colour as a sub-factor. Emergence (up to 35 days after planting), plant height, leaf number, leaf area index, chlorophyll content index and stomatal conductance were measured *in situ*. Yield and yield components were determined at harvest. The Red, Brown and Light-brown landrace selections emerged well, 84, 81 and 51%, respectively. Plant physiological and growth parameters of stomatal conductance, chlorophyll content index, plant height, leaf number, leaf area index and biomass accumulation were lower under rainfed relative to irrigated conditions. Adaptations were landrace selection specific, with Brown and Red landrace selections showing better adaptation to rainfed conditions. Under rainfed conditions, bambara groundnut landrace selections flowered, senesced and matured earlier relative to irrigated conditions. Consequently, there were lower yields under rainfed compared with irrigated conditions. Red and Brown landrace selections may have drought avoidance mechanisms. Seed colour may be used as a selection criterion for drought tolerance in bambara groundnut landraces.

**Keywords:** Bambara groundnut landraces, chlorophyll, drought, LAI, stomatal conductance, yield

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## **Introduction**

Bambara groundnut (*Vigna subterranea* L. Verdc), also known as *Jugo* beans originated in North Africa and migrated with indigenous people to South Africa. It has traditionally been cultivated by women, in extreme tropical environments without access to irrigation and/or

fertilisers and with little guidance on improved practices. Its protein content (16-25%) is reported to rival that of established legumes (Swanevelder 1998, Linnemann and Azam-Ali 1993), making it a good complement for cereal-based diets. However, the promotion of groundnuts (*Arachis hypogaea* L.) has resulted in *Vigna subterranea* being a neglected underutilised species, despite it holding much potential for planting in arid, semi-arid and other marginal production conditions.

In South Africa, bambara groundnut is cultivated under dryland conditions in the KwaZulu-Natal, Mpumalanga, Limpopo and North-West Provinces (Swanevelder 1998). Under these conditions, water stress through insufficient and/or uneven rainfall, remains a significant limitation to crop production. Water stress occurring at any stage can have a negative impact on yield. Several studies described the germination, growth and yield responses of bambara groundnut landraces to water stress (Collinson et al. 1996, 1997, 1999, Sesay et al. 2004, Mwale et al. 2007, Vurayai et al. 2011a, 2011b, Berchie et al. 2012); but information describing local bambara groundnut landraces was scarce.

Collinson et al. (1997) reported that drought tolerance in a Zimbabwean cream bambara groundnut landrace was the result of an ability to maintain leaf turgor pressure through a combination of osmotic adjustment, reduction in leaf area and effective stomatal control. Recently, Jørgensen et al. (2010), working on two bambara groundnut landraces from diverse African origins, re-affirmed this observation. Blum (2005) classified plants that resist drought through enhanced soil water capture, reduced water use and maintaining cellular hydration through osmotic adjustment as drought avoidant. There remains a need to further explore the underlying mechanisms of drought tolerance in bambara groundnut because of the landrace diversity in drought tolerance (Collinson et al. 1997).

There is need to characterise local landraces and identify them for drought tolerance in South Africa. There are currently no improved bambara groundnut cultivars. The crop is sown using landraces, of which little is known regarding their agronomy and water use. Landraces are crop genetic resources that have evolved under natural and farmer practices rather than plant breeding (Zeven 1998). Previous studies have associated seed colour with seed quality and vigour in landraces of maize (Mabhaudhi and Modi 2010, 2011), wild mustard (Mbatha and Modi 2010) and wild water melon (Zulu and Modi 2010), and recently in bambara

groundnut (Sinefu 2011). Although seed coat colour may not necessarily imply genotypic differences, it may be a useful criterion for initial selection of bambara groundnut landraces for improved varieties. This may be especially true for landraces which typically exhibit large variations in seed coat colour but little is known about their seed quality.

In this study, it was hypothesised that local bambara groundnut landraces may have acquired tolerance to drought stress through years of natural and farmer selection under often harsh conditions. It was further hypothesized that such drought tolerance may be linked to seed coat colour. In the process, mechanisms associated with drought tolerance in bambara groundnut would be determined in the context of seed coat colour. Hence, the specific objectives of this study were to evaluate growth, phenological and yield of a local bambara groundnut landrace characterised into three selections according to seed coat colour under irrigated and rainfed field conditions over two seasons.

## **Materials and Methods**

### **Planting material**

Seeds of a locally grown bambara groundnut landrace were collected from subsistence farmers in Jozini (27°26'S; 32°4'E; < 500 masl), northern KwaZulu-Natal, South Africa. The mean annual rainfall for Jozini is > 1000 mm. Information describing the growing period as well as any assumed drought tolerance of the landrace was unavailable. The landrace was characterised into three selections according to seed colour based on previous studies that suggested seed coat colour may have an effect on early establishment performance (Mabhaudhi and Modi 2010, 2011, Mbatha and Modi 2010, Zulu and Modi 2010, Sinefu 2011). The seeds were sorted into three distinct seed coat colours: Red, Brown and Light brown.

### **Description of experimental sites**

Field trials were planted at Roodeplaat, Pretoria (25°60'S; 28°35'E; 1168 masl) during the summer seasons of 2010/11 and 2011/12. During 2010/11, trials were planted on 12

September, 2010 while during 2011/12, trials were planted on 6 September, 2011. The soil was classified as a sandy loam (USDA taxonomic system). The average seasonal rainfall (November to April) of Roodeplaas is ~500 mm, and is highly variable with maximum precipitation in December and January. Daily maximum and minimum temperature averages are 34°C and 8°C, respectively, in summer (November – April) (Agricultural Research Council – Institute for Soil, Climate and Water).

### Experimental design

The experimental design was a split-plot design, with irrigation (full irrigation vs. rainfed) being the main factor and landrace colour being the sub-plot, arranged in a randomised complete block design with three replicates. Main plots were 52 m<sup>2</sup> each with spacing of 10 m between them and sprinklers were designed to have a maximum range of 6 m radius to prevent water sprays from reaching rainfed plots; the sub-plots measured 3 m<sup>2</sup>. Plant spacing was 0.3 m (inter-row) x 0.2 m (intra-row). Trials were irrigated using sprinkler irrigation. Irrigation scheduling, during both seasons, was based on reference evapotranspiration (ET<sub>o</sub>) obtained from an automatic weather station located within a 100 m radius from the experimental site at Roodeplaas, and a crop factor (K<sub>c</sub>). The total amount of rainfall received during the experiments was 678 mm during 2010/11 and 466 mm during 2011/12 growing season. The 2011/12 growing season was characterised by less than average rainfall and was therefore a dry season. Supplementary irrigation supplied to the irrigated treatment amounted to 526 mm during 2010/11 and 890 mm during 2011/12. The higher amount of supplementary irrigation applied during 2011/12 was because this was a drier season compared to 2010/11.

### Agronomic practices

The experiments during 2010/11 and 2011/12 were sown before the onset of the rainy season. Soil samples were obtained from the field trial site prior to planting for determination of soil fertility and texture. Based on soil fertility results, 167 kg N ha<sup>-1</sup>, 23.4 kg P ha<sup>-1</sup> and 78.6 kg K ha<sup>-1</sup> were applied at planting using an organic fertiliser, Gromor Accelerator<sup>®</sup> (30 g kg<sup>-1</sup> N, 15



g kg<sup>-1</sup> P and 15 g kg<sup>-1</sup> K) to meet crop nutritional requirements (Swanevelder 1998). Weeding and ridging were done by hand hoeing.

#### Data collection

Data collection included emergence up to 35 days after planting. Thereafter, plant height, leaf number, leaf area index, stomatal conductance and chlorophyll content index (CCI) were determined either weekly or every fortnight. Crop phenology was observed as days to flowering, flowering duration, days to leaf senescence and days to maturity. A phenological event was deemed to have occurred if it was observed in at least 50% of plants. Days to leaf senescence was described as when at least 10% of leaves had senesced without new leaves being formed to replace them – this stage indicates beginning of canopy decline. Days to maturity was defined in terms of physiological maturity or when at least 50% of leaves in at least 50% of plants had senesced. Leaf area index was measured using the LAI2200 canopy analyser (Li-Cor, USA & Canada). Stomatal conductance was measured using a steady state leaf porometer (Model SC-1, Decagon Devices, USA). Chlorophyll content index was measured using a chlorophyll content meter (CCM-200 *PLUS*, Opti-Sciences, USA); chlorophyll content index data were only measured during the 2011/12 season. Stomatal conductance and CCI were measured from the abaxial (lower) and adaxial (upper) leaf surfaces, respectively, on young fully unfolded leaves. Stomatal conductance was measured on the abaxial surface because it was higher there relative to the adaxial surface. In addition, measurements of stomatal conductance and CCI were taken around midday in-between irrigation and/or rainfall events when the soil was drying. Yield and yield components were determined at harvest. Soil water content was monitored gravimetrically, weekly, at depths of 30 and 60 cm. Weather data for the duration of the experiments was recorded and obtained from the Agricultural Research Council – Institute for Soil, Climate and Water’s automatic weather stations network.

#### Description of statistical analysis

Data were analysed using analysis of variance (ANOVA) (GenStat<sup>®</sup> Version 14, VSN International, UK). Duncan’s multiple range test was used to separate means at the 5% level of significance.

## Results

### Weather conditions

Weather data recorded over the two seasons (2010/11 and 2011/12) showed a significant ( $P < 0.05$ ) difference in rainfall, although temperatures (maximum and minimum) observed were similar (Figure 1). Comparing rainfall received during the two seasons with the average long-term rainfall for Roodeplaat showed that total rainfall received during 2010/11 (766 mm) was 13% more than the long-term rainfall (678 mm). However, in the subsequent season (2011/12), significantly less rainfall was measured (466 mm) compared to the long-term (31% less) and the previous season's rainfall (39% lower).

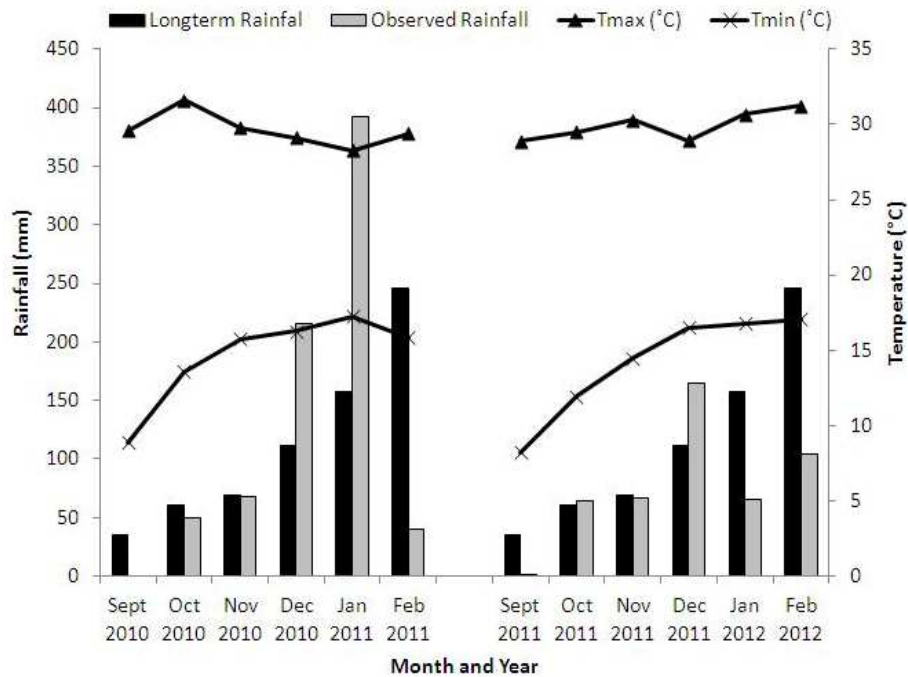


Figure 1: Variations in monthly rainfall and maximum (Tmax) and minimum (Tmin) temperatures (°C) recorded during (A) 2010/11 and (B) 2011/12 planting seasons at ARC-Roodeplaat, Pretoria, South Africa.

## Crop growth

Bambara groundnut landrace selections were slow to emerge. During both the 2010/11 and 2011/12 seasons, it took an average of 35 DAP (days after planting) for the crop to achieve 90% emergence (Figure 2). The trend of slow emergence was consistent over both seasons. During 2010/11, there were highly significant differences ( $P < 0.001$ ) between landrace selections; the 'Brown' landrace had the highest emergence, followed by 'Red' and 'Light brown' landrace selections, respectively. The only difference during 2011/12 was that 'Red' performed better than 'Brown'. However, for both seasons, performance of the 'Light-brown' landrace selection, with regard to emergence, was lesser than that of the darker coloured landrace selections.

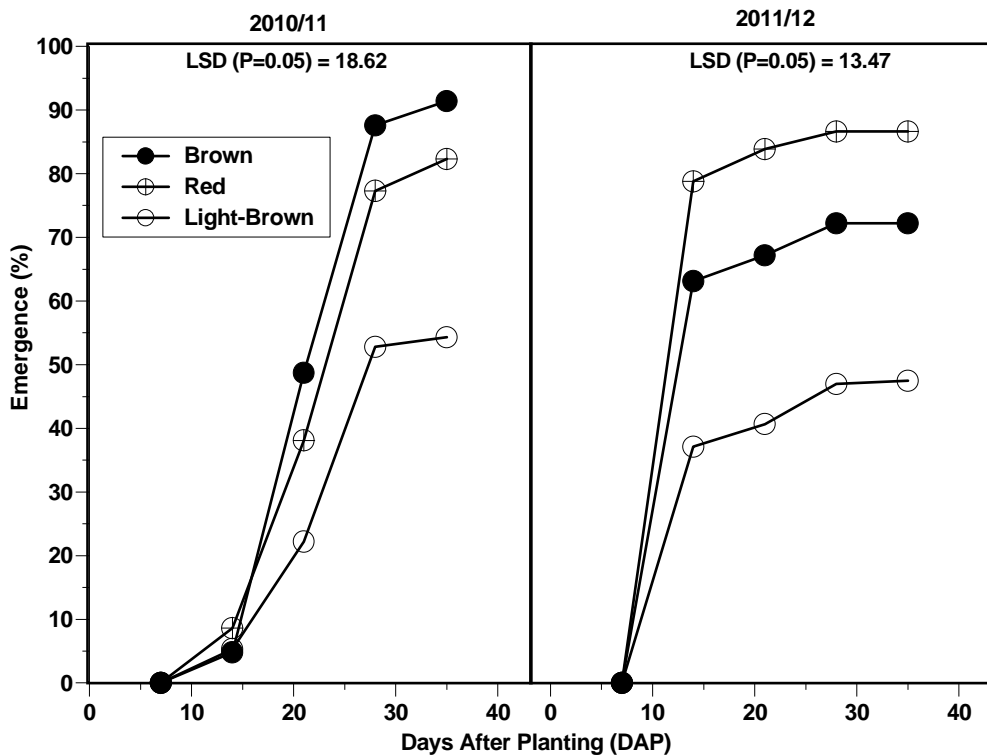


Figure 2: Daily emergence of three bambara groundnut landrace selections (Brown, Red and Light brown) under field conditions during 2011/11 and 2011/12 planting seasons.

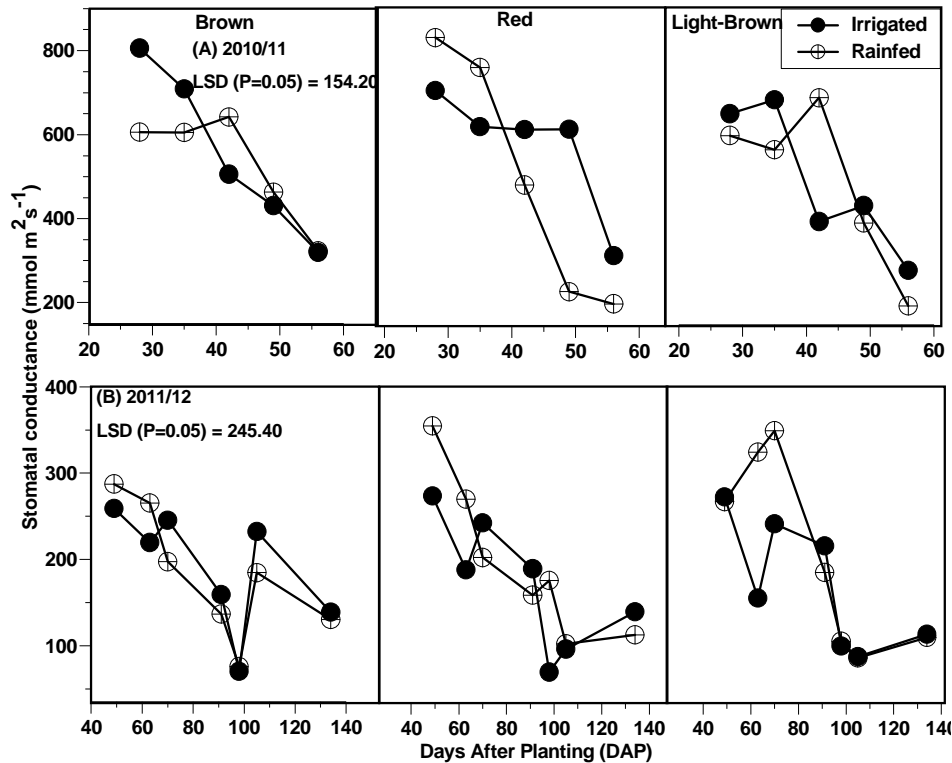


Figure 3: Stomatal conductance ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) of bambara groundnut landrace selections (Brown, Red & Light-brown) under irrigated and rainfed field conditions during 2011/11 and 2011/12 planting seasons. Measurements were taken in-between irrigation and/or rainfall events when the soil was drying.

Although not significantly different, stomatal conductance (SC) was lower under rainfed conditions relative to irrigated conditions (Figure 3). The trend of decline in SC was clearer during 2010/11; under rainfed conditions, SC decreased by 1%, 8% and 6% in ‘Brown’, ‘Red’ and ‘Light-brown’ landrace selections, respectively.

Chlorophyll content index (CCI) was only measured during the 2011/12 season; measurements of CCI were typically observed during periods between irrigation and/or rainfall events when the soil was drying. Results showed significant differences ( $P < 0.001$ ) between rainfed and irrigated water regimes (Figure 4). Chlorophyll content index, on average, was about 25% lower under rainfed conditions relative to irrigated conditions. There were no differences ( $P > 0.05$ ) between landrace selections. The interaction between landrace

and water regime was not significant ( $P > 0.05$ ). The trend in CCI was clearer during the early part of the season. Chlorophyll content index for 'Brown', 'Red' and 'Light-brown' decreased by 29%, 25% and 20%, respectively, under rainfed relative to irrigated conditions.

Plant height and leaf number, observed during 2010/11, showed highly significant differences ( $P < 0.001$ ) between seed colours although there were no significant differences ( $P > 0.05$ ) between water regimes as well as the interaction between landraces and water regime (Figure 5). During 2011/12, results of plant height and leaf number showed highly significant differences ( $P < 0.001$ ) between landraces, water regimes and their interaction (Figure 5). For both seasons, plant height was lower under rainfed conditions compared to irrigated conditions. Leaf number was more affected by water stress than plant height during 2011/12 compared with 2010/11.

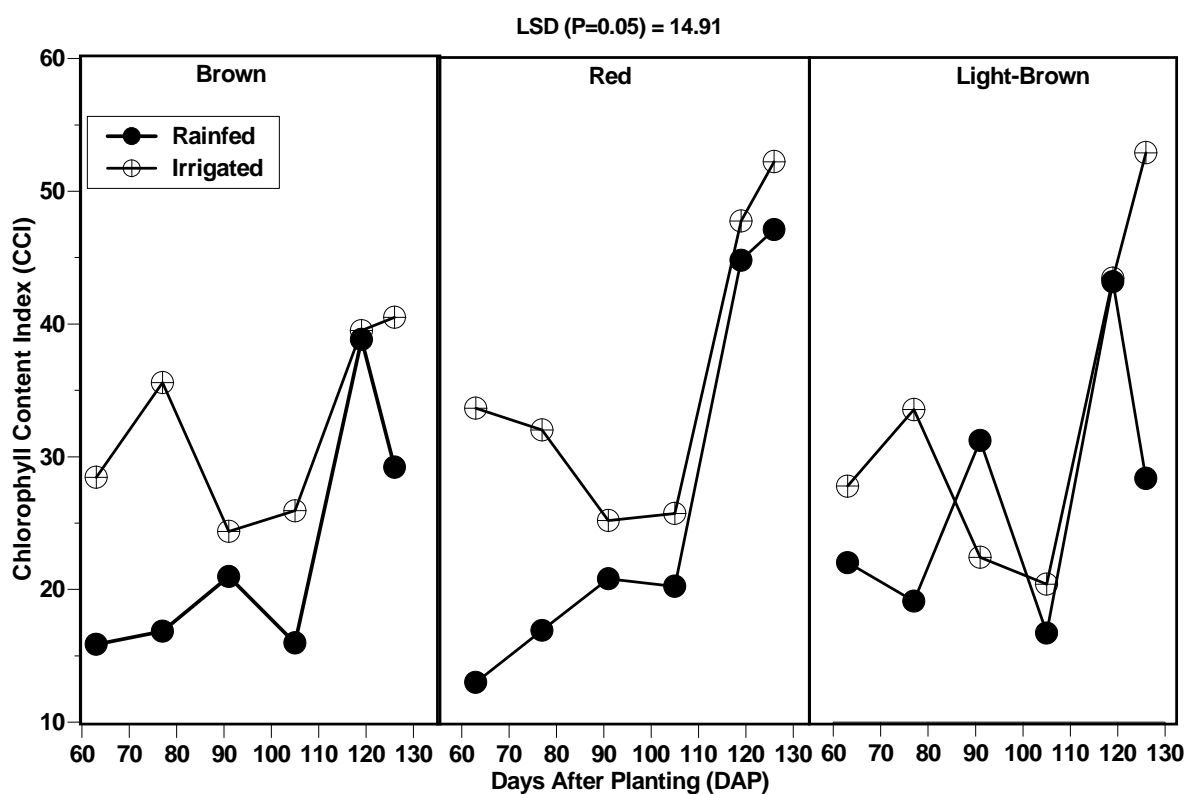


Figure 4: Chlorophyll content index (CCI) of bambara groundnut landrace selections (Brown, Red & Light-brown) under irrigated and rainfed field conditions during the 2011/12 planting season.

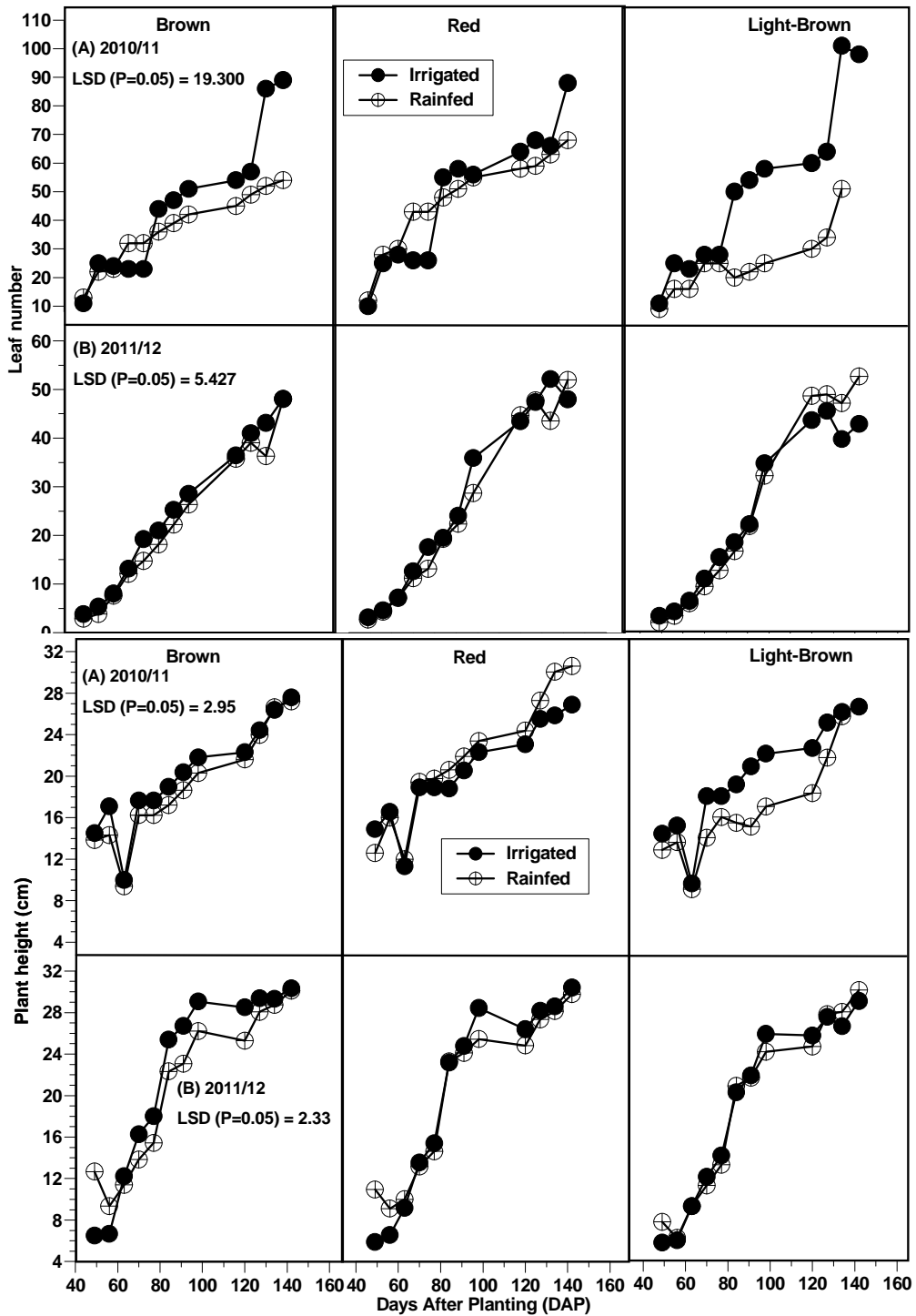


Figure 5: A. Plant height (cm), and B. Leaf number of bambara groundnut landrace selections (Brown, Red & Light-brown) grown under irrigated and rainfed conditions during 2010/11 and 2011/12 planting seasons.

There were no significant differences between landraces or water regimes during 2010/11, with respect to leaf area index (LAI). However, there was a significant interaction ( $P < 0.05$ ) between the two factors. Nonetheless, during 2011/12, there were highly significant differences ( $P < 0.001$ ) between landraces and water regimes (Figure 6). This was consistent with observations of plant height and leaf number during the same season. Based on mean values for landraces across water regimes for both seasons, LAI was lower in ‘Brown’ (18% and 9%) and ‘Red’ (5% and 8%) under rainfed than irrigated conditions (Figure 6).

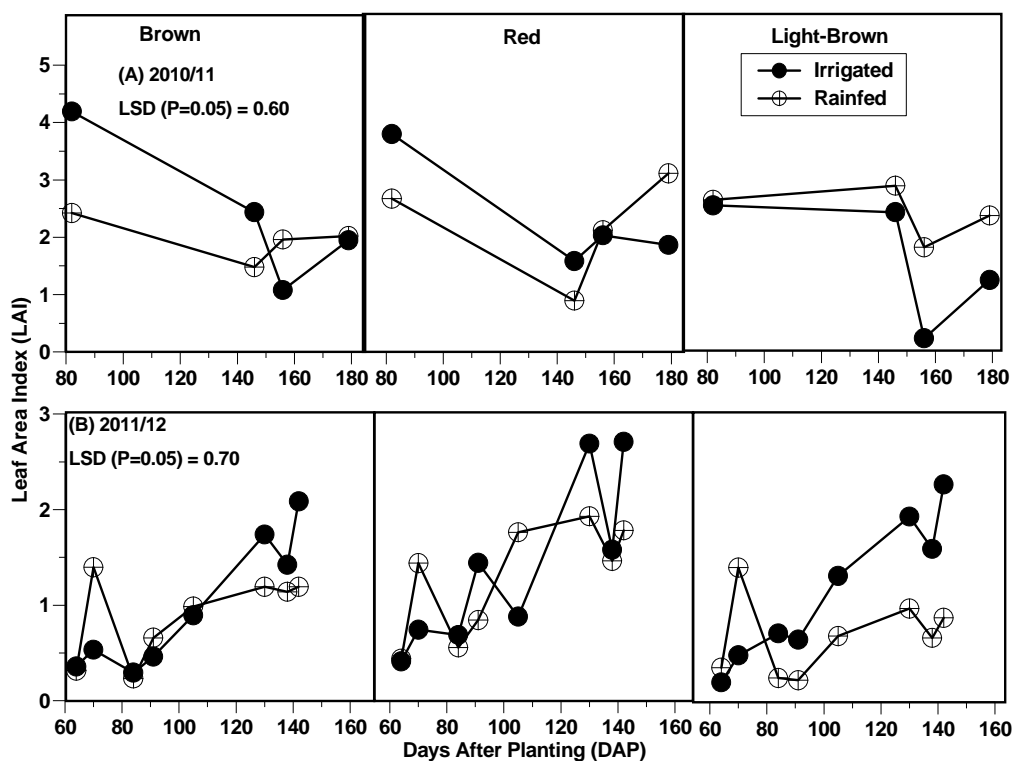


Figure 6: Leaf area index (LAI) of bambara groundnut landrace selections (Brown, Red & Light-brown) grown under irrigated and rainfed conditions during 2010/11 and 2011/12 planting seasons.

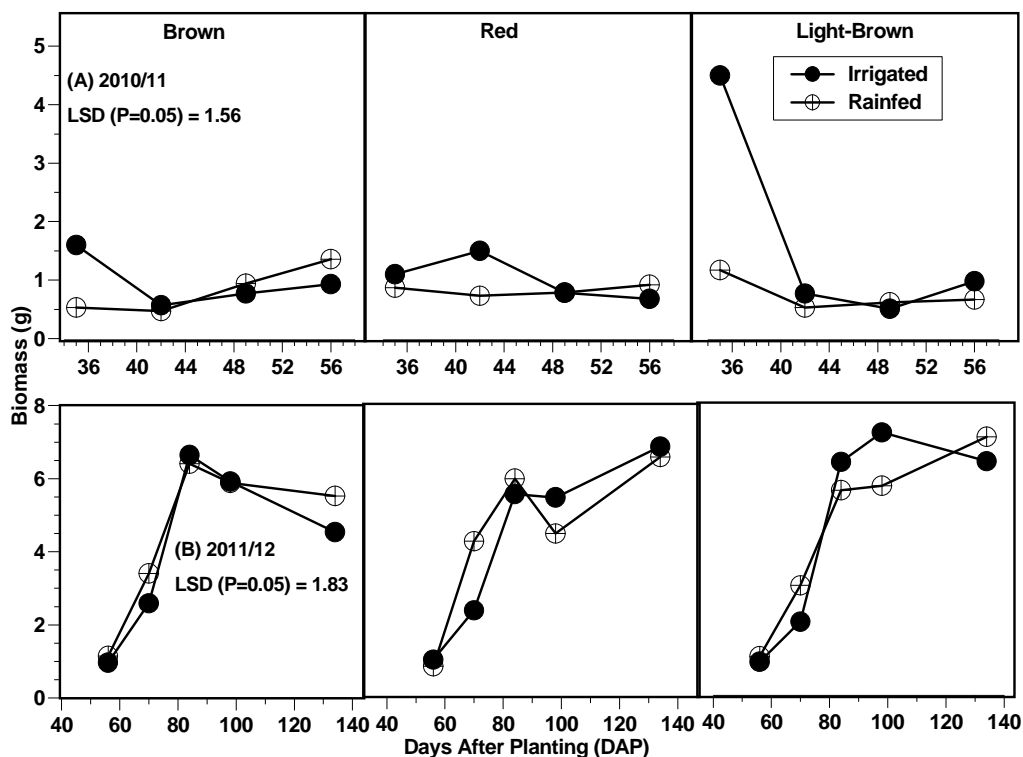


Figure 7: Biomass accumulation (per plant per dry matter basis) of bambara groundnut landrace selections (Brown, Red & Light-brown) grown under irrigated and rainfed conditions during 2010/11 and 2011/12 planting seasons.

Results of biomass accumulation, for both seasons, showed no differences ( $P > 0.05$ ) between landrace selections, water regimes as well as their interaction (Figure 7). However, despite lack of statistical difference, biomass accumulation, with the exception of the 'Light-brown' landrace selection, was lower under rainfed than irrigated conditions (Figure 7).

### Crop phenology

Crop development, defined in terms of occurrence of phenological stages under field conditions, was shown to be significantly affected by different water regimes (Table 1). Days to flowering showed highly significant differences ( $P < 0.001$ ) between landrace selections and between water regimes. Based on mean values for landrace selections, 'Red' flowered earlier than 'Brown' and 'Light-brown', respectively. In addition, mean values for water regimes



showed that flowering occurred earlier (~11 days) under rainfed relative to irrigated conditions. The interaction between landrace and water regime was not significant ( $P > 0.05$ ) for flowering (Table 1).

**Table 1:** Phenological stages of bambara groundnut landrace selections (Brown, Red and Light-brown) grown under irrigated and rainfed conditions during 2010/11 and 2011/12 seasons.

Year	Treatment	Landrace Selection	Flowering g ( <sup>x</sup> DAP*)	Flowering Duration ( <sup>x</sup> Days)	Leaf Senescence ( <sup>x</sup> DAP*)	Maturity ( <sup>x</sup> DAP*)
2010/11 Season	Irrigated	Brown	88ab	47cd	135b	178b
		Red	86bcde	49bc	135b	174c
		Light-brown	93a	47cd	140a	182a
	Rainfed	Brown	75g	39ef	114cd	157d
		Red	72g	43cde	115cd	157d
		Light-brown	82cdef	31g	113d	155e
2011/12 Season	Irrigated	Brown	87bc	56a	143a	150f
		Red	87bc	56a	143a	150f
		Light-brown	87bcd	54ab	141a	148g
	Rainfed	Brown	77fg	40ef	117c	136h
		Red	75g	42de	117c	136h
		Light-brown	81cef	35fg	116cd	134i
LSD <sub>(P=0.05)</sub> Landrace			2.574	2.9	1.5	0.663
LSD <sub>(P=0.05)</sub> Treatment			2.101	2.3	1.2	0.542
LSD <sub>(P=0.05)</sub> Year			2.101	2.3	1.2	0.542
LSD <sub>(P=0.05)</sub> Landrace*Treat*Year			5.147	5.7	3.0	1.326

\*DAP = Days after planting; <sup>x</sup>DAP values were rounded off to the nearest integer. Values in the same column not sharing the same letter differ significantly at LSD ( $P=0.05$ ).

With respect to days to leaf senescence, results showed no significant differences ( $P > 0.05$ ) between landrace selections while there were highly significant differences ( $P < 0.001$ ) between water regimes. Mean values for water regimes showed that under rainfed conditions bambara groundnut landraces flowered at least 15 days earlier than under irrigated conditions. There was no significant ( $P > 0.05$ ) interaction between landrace and water regimes with respect to days to leaf senescence (Table 1).

Flowering duration showed highly significant differences ( $P < 0.001$ ) between landrace selections as well as between water regimes. Based on mean values for landrace selections only, the 'Red' landrace had the longest flowering duration (~48 days) followed by, 'Brown' (~46 days) and 'Light-brown' (~42 days) landrace selections, respectively. Bambara groundnut landrace selections, on average, had a shorter flowering duration under rainfed relative to irrigated conditions. The interaction between landrace and water regime was also significant ( $P < 0.05$ ). 'Brown' and 'Light-brown' landrace selections had the greatest reduction in flowering duration under rainfed compared to irrigated conditions (Table 1).

Days to maturity showed significant differences ( $P < 0.05$ ) between landrace selections and highly significant differences ( $P < 0.001$ ) between water regimes. Means of landraces showed that, on average, 'Red' matured earlier than 'Light-brown' and 'Brown' landrace selections, respectively. Under rainfed conditions, bambara groundnut landrace selections matured earlier (~18 days) than under irrigated conditions. The interaction between landrace and water regime was shown to be highly significant ( $P < 0.001$ ). Although all landrace selections matured earlier under rainfed relative to irrigated conditions, 'Light-brown' and 'Brown' landrace selections matured earlier than the 'Red' landrace selection (Table 1).

## Yield

Results for measured yield components, harvest index (HI), pod mass, pod number per plant, biomass and yield, during the 2010/11 planting season, showed highly significant differences ( $P < 0.001$ ) between water regimes. There were no differences ( $P > 0.05$ ) between landrace selections and the interaction between landrace and water regime was not significant ( $P > 0.05$ ) (Table 2). Harvest index was significantly ( $P < 0.001$ ) lower under rainfed conditions.

This was due to the lower corresponding pod mass (Table 2) under rainfed conditions. The effect of poor podding was shown in yield losses of, on average, 50% for all landraces under rainfed conditions relative to irrigated conditions.

During the 2011/12 season, which was drier than the 2010/11 planting season, results of yield components showed no significant differences ( $P > 0.05$ ) between water regimes and landrace selections; the exception was that for biomass there were significant differences ( $P < 0.05$ ) between water regimes and landrace selections (Table 2). Biomass and yield were significantly lower under rainfed relative to irrigated conditions.

Results of yield components (HI, pod mass, pod number per plant) over the two planting seasons (2010/11 and 2011/12) showed much variability between seasons and landrace selections. Weather data showed that 2011/12 was a drought season with less than average rainfall received. There was a trend of lower HI under rainfed conditions relative to irrigated conditions, for both seasons. Overall, the 'Brown' and 'Red' landraces were more sensitive to lower HI compared with the 'Light-brown' landrace. Despite 2011/12 receiving less than average rainfall, HI under rainfed conditions was higher than during 2010/11, indicating a positive effect of water stress on HI. With respect to final yield, there were highly significant differences ( $P < 0.001$ ) between irrigated and rainfed production, while there were no differences ( $P > 0.05$ ) between the seasons (Table 2). The 'Red' landrace selection, on average, had 3% and 48% higher yield compared with the 'Light-brown' and 'Brown' landrace selections, respectively.

**Table 2:** Yield components of bambara groundnut landrace selections (Brown, Red and Light-brown) grown under irrigated and rainfed conditions during 2010/11 and 2011/12 seasons.

Year	Water	Landrace Selection	HI* (%)	Pod Mass (g plant <sup>-1</sup> )	Pod No. Plant <sup>-1</sup>	Biomass (t ha <sup>-1</sup> )	Yield (t ha <sup>-1</sup> )
2010/11 Season	Irrigated	Brown	25.75abc	21.21ab	25ab	12.98abcd	2.44ab
		Red	31.46ab	24.37a	27ab	11.80bcde	3.34a
		Light-brown	32.46ab	27.53a	35ab	16.79a	3.22ab
	Rainfed	Brown	6.21c	4.27b	10b	10.60bcde	0.66c
		Red	17.48bc	12.94ab	17ab	11.69bcde	1.52bc
		Light-brown	13.29bc	9.89ab	15ab	14.81ab	1.43bc
<b>LSD<sub>(P=0.05)</sub> Landrace*Water (2010/11)</b>			<b>9.22</b>	<b>11.76</b>	<b>17.16</b>	<b>3.722</b>	<b>1.359</b>
2011/12 Season	Irrigated	Brown	32.61ab	16.04ab	21ab	8.23de	2.28abc
		Red	30.75ab	22.35a	32ab	12.14abcde	2.84ab
		Light-brown	20.76bc	20.74ab	36a	13.44abc	2.60ab
	Rainfed	Brown	25.19abc	11.66ab	15ab	7.90de	1.62abc
		Red	30.36ab	15.26ab	22ab	8.75cde	1.84abc
		Light-brown	42.11a	23.22a	24ab	10.23bcde	1.99abc
<b>LSD<sub>(P=0.05)</sub> Landrace*Water (2011/12)</b>			<b>18.809</b>	<b>11.042</b>	<b>19.876</b>	<b>4.331</b>	<b>1.085</b>
<sup>z</sup> Yield correlation (r)			0.657	0.873	0.860	0.396	-----
<sup>z</sup> LSD <sub>(P=0.05)</sub> Landrace			8.949	7.582	11	2.192	0.775
<sup>z</sup> LSD <sub>(P=0.05)</sub> Treatment			7.307	6.191	9	1.790	0.633
<sup>z</sup> LSD <sub>(P=0.05)</sub> Year			7.307	6.191	9	1.790	0.633
<sup>z</sup> LSD <sub>(P=0.05)</sub> Landrace*Treat*Season			17.898	15.164	21	4.384	1.549

\*HI = harvest index; <sup>x</sup> Pod number per plant values were rounded off to the nearest integer since pod number represents discrete data. Values in the same column not sharing the same letter differ significantly at LSD (P=0.05). Mean separation was done using the LSD value for the Landrace selection\*Treatment\*season interaction. <sup>z</sup>Statistics refer to the comparison between the 2010/11 and 2011/12 planting seasons for the three bambara groundnut landrace selections under irrigated and rainfed conditions.

## **Discussion**

Bambara groundnut landrace selections were slow to emerge under both irrigated and rainfed conditions, taking an average of 28-35 DAP to emerge. This was much longer than the 7-14 days reported by Swanevelder (1998). Slow emergence observed in this study may be due to poor seed quality of landraces used in this study. Landraces often lack the same vigour as hybrids or other improved varieties (Mabhaudhi and Modi, 2010). Thence, there is a need to come up with strategies to improve or enhance seed quality in landraces. In a study on maize landraces, Mabhaudhi and Modi (2011) showed hydropriming could be used to improve seed vigour and emergence of maize landraces.

In addition, slow emergence may have been the result of planting early in September when temperatures were still relatively cool. Sinefu (2011) observed similar results showing that bambara groundnut landraces were slow to emerge (taking up to 35 DAP) for trials planted in September (early); emergence improved with later plantings in November and January when temperatures were warmer.

The fact that 'Red' and 'Brown' landrace selections consistently emerged better than 'Light-brown'; further strengthens our initial hypothesis that darker coloured seeds may have better vigour compared with light coloured seeds (Mabhaudhi and Modi 2010, Zulu and Modi 2010, Mbatha and Modi 2010). The effect of seed coat colour on seed quality has previously been related to levels of phenolic compounds (Anuradha et al. 2009) and seed coat thickness (Sinefu 2011). Darker coloured seeds may contain high levels of phenolic compounds (Anuradha et al. 2009). High phenolic content in darker coloured seeds may be the reason for the association between dark seed colour and seed quality since phenolic compounds have antioxidant properties. As such, seed coat colour may be a useful indicator of seed quality (Anuradha et al. 2009).

Although our results of stomatal conductance were not statistically significant, stomatal conductivity was lower under rainfed than irrigated conditions. Under water limited conditions, stomatal closure is designed to reduce water losses through transpiration. This means that the bambara groundnut landrace selections used in this study were able to adapt to limited water availability under rainfed conditions by closing their stomata. The fact that stomatal conductance was lower under rainfed relative to irrigated conditions implies that

bambara groundnut landraces demonstrated a degree of stomatal control hence regulation of transpirational losses. Stomatal closure is widely thought to be a plant's first line of defence in response to developing water stress (Mansfield and Atkinson 1990, Cornic and Massacci 1996). Similar observations of stomatal regulation in bambara groundnut were reported by Collinson et al. (1997). They stated that drought tolerance in bambara groundnuts may be due to greater stomatal regulation which is a drought avoidance mechanism. Recently, Jørgensen et al. (2010) observed stomatal closure in two bambara groundnut landraces from two diverse locations in Africa. They also concluded that stomatal closure in bambara groundnut was an important strategy for survival during intermittent stress.

In addition to reducing transpiration, stomatal closure also decreases flow of CO<sub>2</sub> into leaves, followed by a parallel decline in net photosynthesis, ultimately resulting in reduced plant growth. Decreased CO<sub>2</sub> availability necessitates a down-regulation of photosynthesis. This involves lowering the levels of photosynthetic pigments, chiefly - chlorophyll. Results of this study showed that chlorophyll content was lower in rainfed plants relative to irrigated plants. Chlorophyll content of 'Brown', 'Red' and 'Light-brown' landrace selections was respectively 29%, 25% and 20% lower under rainfed than irrigated conditions. 'Brown' and 'Red' landrace selections were therefore shown to be able to reduce chlorophyll content better than the 'Light-brown' landrace selection. Reduction in chlorophyll content, results in less energy captured for photosynthesis. If this down-regulation was not to occur, the plant would have more energy than required to fix CO<sub>2</sub> resulting in increased levels of free radicals which would in turn damage the chloroplast membranes (Chaves and Oliveira 2004). As such, bambara groundnut landraces demonstrated an ability to down-regulate photosynthesis in line with reduced CO<sub>2</sub> availability caused by stomatal closure. Several experiments conducted on barley (Anjum et al. 2003) and sunflower (Kiani et al. 2008, Farooq et al. 2009) also showed that water stress decreased chlorophyll content.

Rainfed production led to lower plant height, leaf number and LAI relative to irrigated conditions. On average, irrigated plants were shown to have taller plants, greater leaf number and LAI relative to rainfed plants. Although there was much variability within and between landrace selections, 'Brown' and 'Red' landrace selections responded to rainfed production by reducing their canopy size as defined by plant height, leaf number and LAI. Canopy size

results during 2010/11 showed no differences between water treatments in the field trials due to a favourable rainfall season; however, there were differences during 2011/12 when rainfall was below the long-term average. The lower plant growth observed under rainfed conditions may have been due to reduced photosynthesis emanating from reduced CO<sub>2</sub> assimilation and fixation due to stomatal closure and reduced chlorophyll in the leaves. Plants, by nature, are designed to reduce water use when confronted with water stress (Blum 2005). Reduced plant height, leaf area and LAI constitute this adaptation aimed at minimising water loss under drought stress (Mitchell et al. 1998). Similar results showing reduction in plant height, leaf number and LAI were found in the literature (Collinson et al. 1996, 1997, 1999, Sesay et al. 2004, Mwale et al. 2007, Vurayai et al. 2011a, 2011b, Berchie et al. 2012).

Results of biomass accumulation and final biomass showed that, despite much variability between the landrace selections, there was a trend of declining biomass under rainfed relative to irrigated conditions. Such a trend was consistent with the trend observed for stomatal conductance, chlorophyll content and plant growth parameters. The combination of reduced CO<sub>2</sub> assimilation, low chlorophyll content and a smaller canopy size ultimately meant that bambara groundnut landrace selections produced less biomass under rainfed relative to irrigated conditions. This explains why researchers have previously ascribed stomatal limitations to photosynthesis as the chief yield limiting factor under conditions of limited water availability (Cornic and Massacci 1996, Chaves et al. 2002, 2003, Yokota et al. 2002). Blum (2005) stated that drought avoidance mechanisms had the down side of reduced biomass production. This is because in order for the plant to avoid drought, it would require to minimise water losses through stomatal closure and reduced canopy size, both of which ultimately reduce the amount of biomass produced by the plant.

Another important plant response to water limited conditions is the timing and duration of key phenological events such as flowering. In the current study, results of crop phenology showed clear responses, with regards to bambara groundnut landrace selections' responses to rainfed production. Under rainfed conditions, bambara groundnut landrace selections flowered much earlier, had a shorter flowering duration, and matured earlier relative to irrigated conditions. This trend was more lucid during the 2011/12 season which was a dry season. In the case of the 'Brown' and 'Light-brown' landrace selections, these observations may have

been due to enhanced leaf senescence under rainfed conditions. Although the 'Red' landrace selection flowered early, it was shown to senesce later, compared with the 'Brown' and 'Light-brown' landrace selections; this phenomenon may also suggest delayed leaf senescence in the 'Red' landrace selection. Odindo (2007) also observed delayed leaf senescence in water stressed cowpeas. Blum (2005) stated that early flowering, partly due to reduced growth duration (leaf number and area), was a major mechanism for moderating water loss under drought stress. Early flowering has been classified as a drought escape mechanism (Araus et al. 2002). However, a crop that escapes drought cannot attain maximum yield under water stress (Blum 2005) due to reduced crop duration.

Results for measured yield components HI, pod mass, pod number per plant and yield showed much variability within landraces over the two seasons. Harvest index was lower under rainfed relative to irrigated conditions; this was due to corresponding low pod number and mass as well as total biomass under rainfed conditions. This resulted in yield losses of, on average, 50% for all landraces under rainfed conditions during 2010/11. Nonetheless, the 'Red' landrace selection consistently performed well under all conditions and hence may be described as the most stable of the three seed colour selections. The seemingly better performance of the 'Red' landrace selection may be linked to its ability to regulate stomatal closure, moderate reductions in chlorophyll content and phenological plasticity. Of the three landrace selections, the 'Red' landrace selection showed delayed leaf senescence under rainfed production, an adaptation that allowed it to have a longer flowering duration and build-up of harvest index. Blum (2005) stated that crops that avoided drought through stomatal regulation, reduced plant size, LAI, and growth duration due to early flowering, did so at the expense of attaining high yields. Jaleel et al. (2009) stated that crops showed variation in yield under stress while Jørgensen et al. (2011) noted that the variability that exists within bambara groundnut landraces necessitated the need for more research on drought tolerance. Such variability may be a reason for low yields and may explain why farmers do not cultivate bambara groundnut extensively. Our results of reduced yield under rainfed conditions concur with other reports in the literature where limited water availability was shown to reduce yield of bambara groundnuts (Mwale et al. 2007, Sinefu 2011, Vurayai et al. 2011b). In addition, values of HI observed in this study for the 'Red' and 'Brown' landrace selections were similar to those reported by Mwale et al. (2007).



Pod number, pod mass and HI, respectively, were shown to contribute significantly to yield attainment or loss. Bambara groundnut landrace selections yielded significantly better under rainfed conditions during 2011/12 which was a drier season compared to 2010/11. The above average rainfall received during 2010/11 may have resulted in periods of intermittent water logging. Since bambara groundnut is sensitive to water logging (Swanevelder, 1998), this could have resulted in yield losses during 2010/11. These results agree with reports in the literature that bambara groundnut is drought tolerant and will give reasonable yield under drought stress (Harris and Azam-Ali 1993).

### **Conclusion**

Bambara groundnut landrace selections demonstrated drought avoidance and escape mechanisms under rainfed cultivation compared with irrigated conditions. Bambara groundnut landrace selections avoided drought by minimising water losses through stomatal closure, reducing plant height, leaf number and LAI in response to reduced water availability under rainfed conditions. Chlorophyll content index proved to be a useful index for evaluating crop responses to reduced water availability under rainfed conditions. It was lower under rainfed conditions relative to irrigated conditions, at least earlier in the season. However, CCI was only observed during 2011/12 hence more research is necessary on this trait. Flowering was hastened, the duration of flowering was shortened, leaf senescence started sooner, and crop duration, as shown by days to maturity, was shortened under rainfed conditions relative to irrigated conditions. Thus, bambara groundnut shows a degree of phenological plasticity in response to drought. Biomass, harvest index and seed yield were all lower under rainfed conditions relative to irrigated conditions. 'Red' and 'Brown' landrace selections showed better resilience to drought stress compared with the 'Light-brown' landrace selection. While seed coat colour does not imply genotypic differences, it may be used as a selection criterion for identifying bambara groundnut landraces with potential for water stress tolerance.

## **Acknowledgements**

Water Research Commission of South Africa K5/1771/4. Water-Use of Drought Tolerant Crops. WRC Knowledge Review 2008-09.

## **References**

**(See final reference list pages 198-228)**

## CHAPTER 6

### **Growth, phenological and yield responses of a bambara groundnut (*Vigna subterranea* L. Verdc) landrace to imposed water stress: II. Rain shelter conditions**

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## **Abstract**

Bambara groundnut is a protein-rich legume, with food security potential. Effects of irrigation levels and seed coat colour on growth, development, yield and water-use efficiency of local bambara groundnut landrace selections were evaluated under a rain shelter. Emergence was slow, although variation was indicated between landraces. Limited water availability was shown to lower stomatal conductance, although chlorophyll content index was shown to be unaffected. Additionally, growth indices of plant height, leaf number and leaf area index were shown to be lower in response to decreasing water availability. Furthermore, landraces generally flowered and matured earlier while also demonstrating higher water-use efficiency at lower water availability. Seed yield was lower under limited water availability resulting from lower pod mass and pod number. Drought tolerance in bambara groundnut landraces was achieved by reducing canopy size, early flowering and maturity, and maintaining high water use efficiency under stress. 'Brown' and 'Red' landraces responded to water stress better than the 'Light-brown' landrace, suggesting an effect of seed colour on possible drought tolerance.

**Keywords:** bambara groundnut landrace, growth, phenology, water use efficiency, yield

## Introduction

South Africa is a water-scarce country (International Water Management Institute, 1996; Republic of South Africa Water Act, 1998; Department of Water Affairs and Forestry, 2002; The Water Wheel, 2007) due to a limited amount of water resources combined with low and uneven annual rainfall (Laker, 2007), which often results in drought. The marginal nature of most of South Africa and expected climate change (Hassan, 2006) challenge the existence of major crops and their ability to ensure food security in the future. Neglected underutilised species (NUS) have been reported to have possibly evolved to tolerate harsh environments, including drought stress, and have been touted as possible future (food security) crops. Bambara groundnut (*Vigna subterranea* (L.) Verdc), locally known as *Izindlumbu* in isiZulu, is one such indigenous legume with potential to contribute nutritional and food security in marginal areas of agricultural production.

Bambara groundnut is an African indigenous legume that has been cultivated for centuries in sub-Saharan Africa, mainly the semi-arid regions, and has in the past contributed to food security (Swanevelder, 1998; FAO, 2001; Azam-Ali et al., 2001; Mwale et al., 2007). Traditionally, it was cultivated in extreme, tropical environments by small-scale farmers without access to irrigation and/or fertilisers and with little guidance on improved practices. It is mainly grown by women for the sustenance of their families (Mukurumbira, 1985; Mwale et al., 2007). It has been reported to contain 17-25% protein, 42-65% carbohydrate and 6% lipid (Aykroyd and Doughty, 1982; Linnemann and Azam-Ali, 1993; Mwale et al., 2007). However, germplasm improvement and management practices have mainly relied on local experience and resources (indigenous knowledge) (Mukurumbira, 1985). Consequently, the crop remains underutilised and is still mainly cultivated from landraces of which very little is known about their growth, yield and water-use responses under water stress conditions.

There is hardly any report in literature describing water-use efficiency of bambara groundnut. The growth responses of bambara groundnut to water stress have been described in several instances, using growth indices such as plant height, leaf area index and total dry matter (Collinson et al., 1996, 1997, 1999; Mwale et al., 2007; Vurayai et al., 2011a, 2011b). However, most of this research has been done under controlled environments (Sesay et al., 2010) and field conditions whereby quantifying water was not the major objective. Water use

efficiency has often been equated to high yield potential under optimum and stressful conditions (Blum, 2005). Reduced plant canopy size and maturity are often associated with increased water use efficiency and better drought tolerance in plants although literature has shown that there may be yield penalties; however, little is currently known of this relationship in local bambara groundnut landraces. Therefore, the objective of the current study was to evaluate growth, development, yield and water-use efficiency of local bambara groundnut landraces characterised according to seed coat colour to water stress under rain shelter conditions.

## **Experimental**

### ***Plant material***

Fresh seeds of local bambara groundnut landraces were collected from subsistence farmers in Jozini (27°26'S; 32°4'E), northern KwaZulu-Natal, South Africa in 2010. The same seed lot was used for both seasons during which the trials were conducted. Seeds were characterised according to seed coat colour and sorted into three distinct seed coat colours: 'Red', 'Brown' and 'Light brown'. Seed characterisation according to seed colour was based on the hypothesis that dark coloured seeds tend to be more vigorous than light coloured seeds and may thus be more drought tolerant compared with light coloured seeds (Mabhaudhi and Modi, 2010, 2011; Mbatha and Modi, 2010; Zulu and Modi, 2010).

### ***Site descriptions***

Trials were planted at Roodeplaat, Pretoria (25°60'S; 28°35'E) during the summer seasons of 2010/11 and 2011/12. Soils in the rain shelters were classified as loamy sand (USDA taxonomic system). Soil physical characteristics were used to generate parameters for amount of water available at field capacity (FC), permanent wilting point (PWP), and saturation (SAT), as well as the saturated hydraulic conductivity using the Soil Water Characteristics Hydraulic Properties Calculator<sup>®</sup> (Version 6.02.74, USDA Agricultural Research Services). Daily maximum and minimum temperature averages are 28.5°C and 15°C in summer

(November – April) (Agricultural Research Council – Institute of Soil Climate and Weather). Rainfall was excluded since the rain shelters are designed to close when rainfall starts.

### ***Experimental designs***

The experimental design was a factorial experiment arranged in a completely randomised block design; individual plot size in the rain shelter was 6 m<sup>2</sup>, with plant spacing of 0.3 m x 0.3 m. There were two factors: irrigation level and seed colour, replicated four times. During the 2010/11 season, only two seed colours, ‘Brown’ and ‘Red’, were used in the rain shelter experiments. However, in the subsequent season, 2011/12, all three colours (‘Brown’, ‘Red’ and ‘Light-brown’) were used. There were three irrigation levels 30%, 60% and 100% of crop water requirement (ET<sub>a</sub>) calculated using reference evapotranspiration (ET<sub>o</sub>) and a crop factor (K<sub>c</sub>) as described by Allen et al. (1996):

$$\mathbf{ETa = ET_o * K_c}$$

where, ET<sub>a</sub> = crop water requirement

ET<sub>o</sub> = reference evapotranspiration, and

K<sub>c</sub> = crop factor.

### ***Irrigation***

Drip irrigation was used to apply water in the rain shelter. The system consisted of a pump, filters, solenoid valves, water meters, control box, online drippers, 200 litre JOJO tank, main line, sub-main lines and laterals. The system was designed to allow for a maximum operating pressure of 200 kPa with average discharge of 2 l/hour per emitter. Drip lines were spaced according to the plant spacing (0.3 m x 0.3 m). A black 200 µm thick polyethylene sheet was trenched at a depth of 1 m to separate the plots in order to prevent water seepage and lateral movement of water between plots. Irrigation scheduling was based on reference evapotranspiration (ET<sub>o</sub>) and a crop factor (K<sub>c</sub>).

### ***Data collection***

**Plant measurements:** Parameters determined weekly were emergence [up to 35 days after planting (DAP)], plant height, leaf number, leaf area index (LAI), stomatal conductance (SC), chlorophyll content (CC) and days to flowering (DTF). At the end of the season, biomass and yield were determined. Whereas data for growth parameters were collected weekly from 35 DAP, destructive sampling was performed biweekly to determine dry mass. Leaf area index was measured using the LAI2200 Canopy Analyser (Li-Cor, USA & Canada). Stomatal conductance was measured using a steady state leaf porometer (Model SC-1, Decagon Devices, USA). Chlorophyll content was measured using a Chlorophyll content meter (CCM-200 *PLUS*, Opti-Sciences, USA); CC data were only measured during the 2011/12 season.

**Soil water content (SWC):** during the 2010/11 season, a neutron water meter was used to determine SWC at soil depths of 20, 40, 60, 80 and 100 cm, at weekly intervals. Wet and dry spot readings were determined, together with their corresponding volumetric water contents in order to obtain a best-fit regression equation (Campbell and Mulla, 1990). The equation was then used to develop a spreadsheet for the conversion of neutron probe readings to corresponding volumetric SWC readings. During the 2011/12 season, ML-2X Theta Probes connected to a DL-6 data logger (Delta-T Devices, UK) were used to monitor SWC in the rain shelters at varying depths. The frequency of data collection for SWC using the Theta probes was every 4 hours.

**Water-use efficiency (WUE):** water-use efficiency for the crop was determined as follows:

$$WUE = \frac{Biomass}{ET_a}$$

where: WUE = water-use efficiency, and

ET<sub>a</sub> = crop water requirement.



### ***Agronomic practices***

Prior to planting, soil samples were obtained from the rain shelter for determination of soil fertility and texture. Based on soil fertility results, an organic fertiliser, Gromor Accelerator<sup>®</sup> was applied at planting to meet crop nutritional requirements (Swanevelder, 1998). Routine weeding and ridging were done by hand.

### ***Data analysis***

Analysis of variance (ANOVA) was used to statistically analyse data using GenStat<sup>®</sup> (Version 14, VSN International, UK). Least significant difference (LSD) was used to separate means at the 5% level of significance.

## **Results and discussion**

### ***Crop establishment***

During the 2010/11 season, results of emergence showed significant differences ( $P < 0.05$ ) between the 'Red' and 'Brown' landraces, with 'Red' emerging better than 'Brown' (data not shown because only two landrace selections were used). During the 2011/12 season, results showed highly significant differences ( $P < 0.001$ ) between landraces, with 'Brown' and 'Red' having higher and faster emergence compared with the 'Light-brown' landrace (Figure 1). These results suggest a possible effect of seed colour on vigour. Over-all, for both seasons, time to 90% emergence was generally achieved 28 days after sowing, indicating that bambara groundnut landraces are slow to establish as reported by Sinefu (2011). Successful crop establishment is critical under water limited conditions; Blum (2009) stated that during crop establishment a significant amount of total available water is lost through soil evaporation not transpiration. Therefore, a significant amount of water is probably lost due to soil evaporation with this slow establishment in bambara groundnut. Researchers in Australia, working on wheat, found that about 40% of total available water was lost to soil evaporation at establishment stage (French and Schultz, 1984; Siddique et al., 1990). Vigorous seedling growth is thus essential in establishing canopy cover and reducing water losses to evaporation; this is now a part of an Australian wheat breeding program (Rebetzke and Richards, 1999).

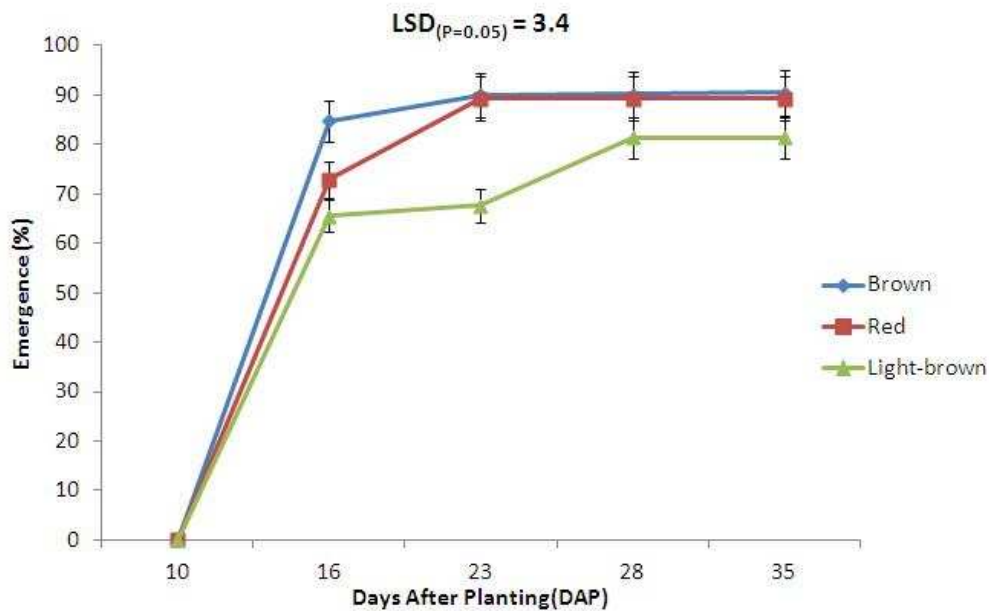


Figure 1: Emergence of bambara groundnut landraces ('Brown', 'Red' and 'Light brown') under rainshelter conditions during 2011/12 planting season.

### ***Crop physiology: Stomatal conductance and chlorophyll content***

Closure of stomata reduces transpirational losses, thus minimising water losses through transpiration while also lowering photosynthesis. Results of stomatal conductance (SC) were only collected during the 2011/12 planting season. The results showed highly significant differences ( $P < 0.001$ ) between water regimes as well as significant differences ( $P < 0.05$ ) between landraces (Figure 2). The trend showed that SC decreased with increasing water stress (Figure 2). 'Red' and 'Brown' landraces showed the greatest decrease in response to water stress compared with the 'Light-brown' landrace (Figure 2), demonstrating greater stomatal regulation in response to water stress. Stomatal closure is a plant's initial response to declining soil water content and has been characterised as a drought avoidance mechanism (Farooq et al., 2009) as well as being a characteristic of increased water use efficiency under drought stress (Blum, 2005, 2009). It has previously been suggested as a component of bambara groundnut's drought resistance mechanisms by Collinson et al. (1997). However, Blum (2005, 2009) argued that stomatal closure is a negative response to water stress in that it reduces  $\text{CO}_2$  availability leading to yield reduction under water stress.

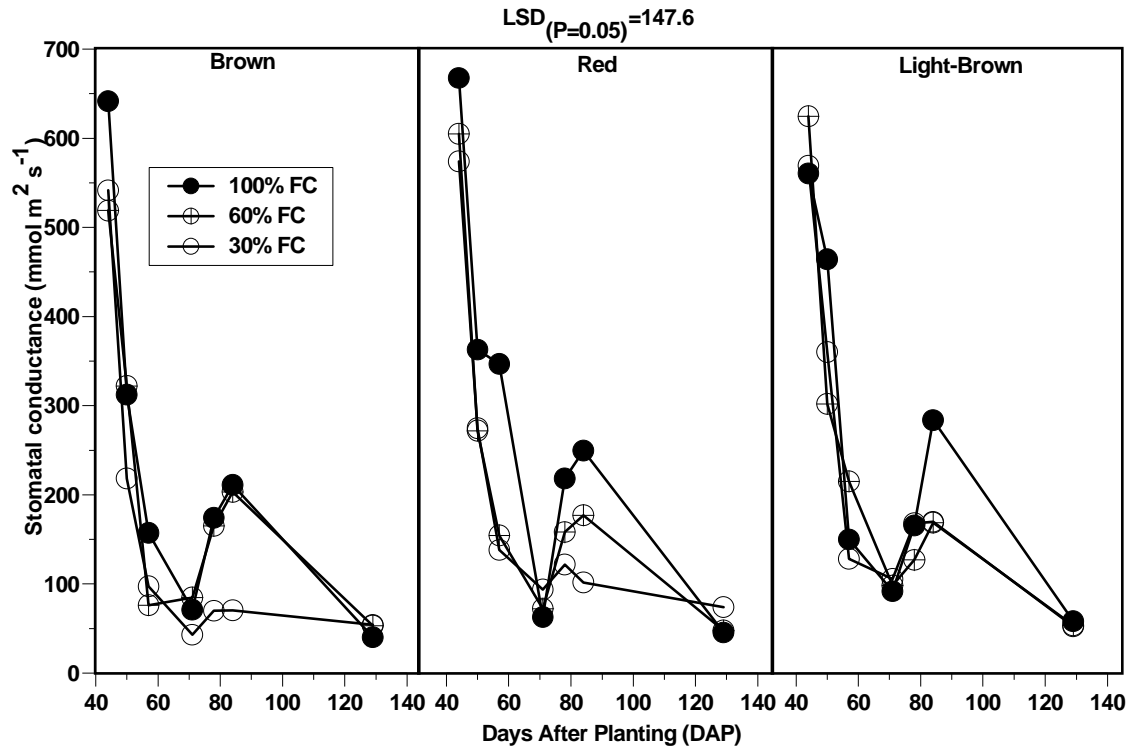


Figure 2: Stomatal conductance ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) of bambara groundnut landraces ('Brown', 'Red' and 'Light brown') grown under a rainshelter during the 2011/12 planting season.

Reduction in intracellular CO<sub>2</sub>, due to stomatal closure, results in reduced substrate availability for photosynthesis. Therefore, there is need to down-regulate photosynthesis in line with reduced substrate availability. In this regard, chlorophyll content has been reported to decrease in water stressed plants (Farooq et al., 2009), for example, in barley (Anjum et al., 2003) and sunflower (Kiani et al., 2008). Results of chlorophyll content index were only collected during the 2011/12 planting season. There were no significant differences ( $P > 0.05$ ) between landraces, water regimes as well as their interaction (Figure 3); suggesting that chlorophyll content in bambara groundnut landraces was not sensitive to water stress. Interestingly, with the exception of the ‘Light-brown’ landrace, ‘Red’ and ‘Brown’ had higher CCI at 30% ETa relative to 60% ETa, whilst all landraces had highest CCI at 100% CCI (Figure 3). These results once again showed the variability that exists within landraces, with respect to responses to water stress.

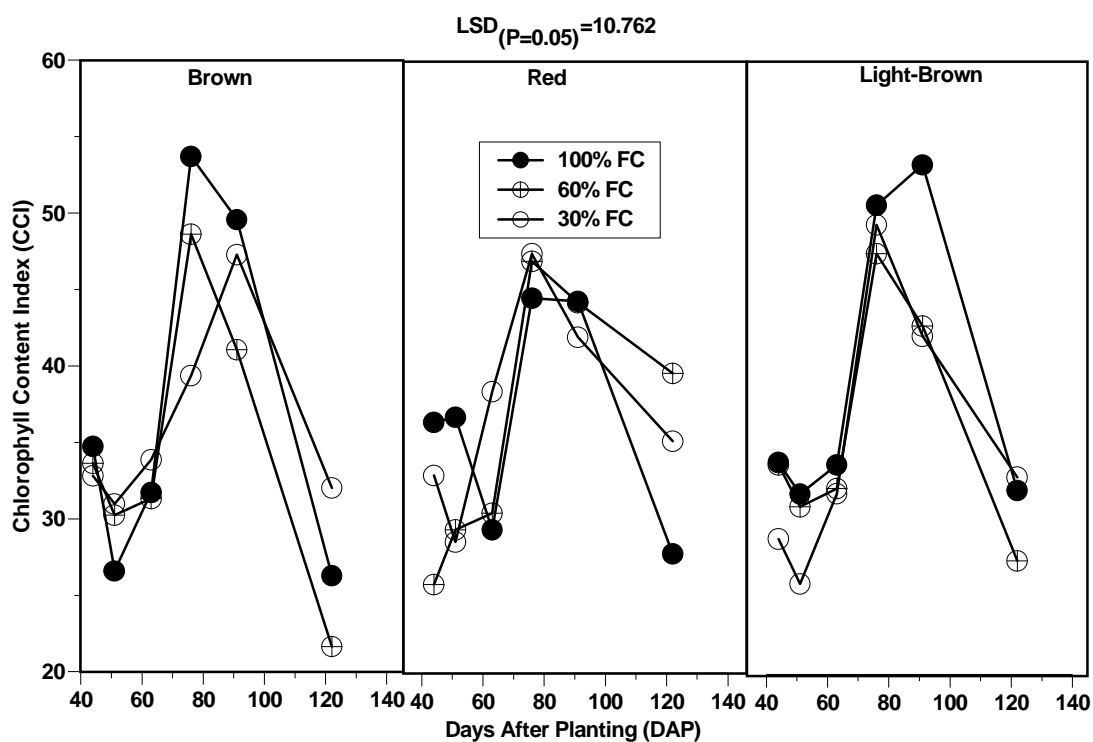


Figure 3: Chlorophyll content index (CCI) of bambara groundnut landraces (‘Brown’, ‘Red’ and ‘Light brown’) grown under a rainshelter during the 2011/12 planting season.

## Crop growth

Results of plant height and leaf number during 2010/11 and 2011/12 were variable (Figures 4 & 5), with respect to differences between water regimes and landraces. In the 2011/12 season, the 'Light-brown' landrace performed better than the 'Brown' and 'Red' landraces, respectively. There was a trend, for both seasons, of decreasing plant height and leaf number in response to increasing water stress. The lowest values of plant height and leaf number were observed in the 30% ETa treatment, followed by 60% and 100% ETa, respectively. The 'Red' landrace was shown to have the greatest decrease in plant height and leaf number under water stress compared with 'Light-brown' and 'Brown' (Figures 4 & 5).

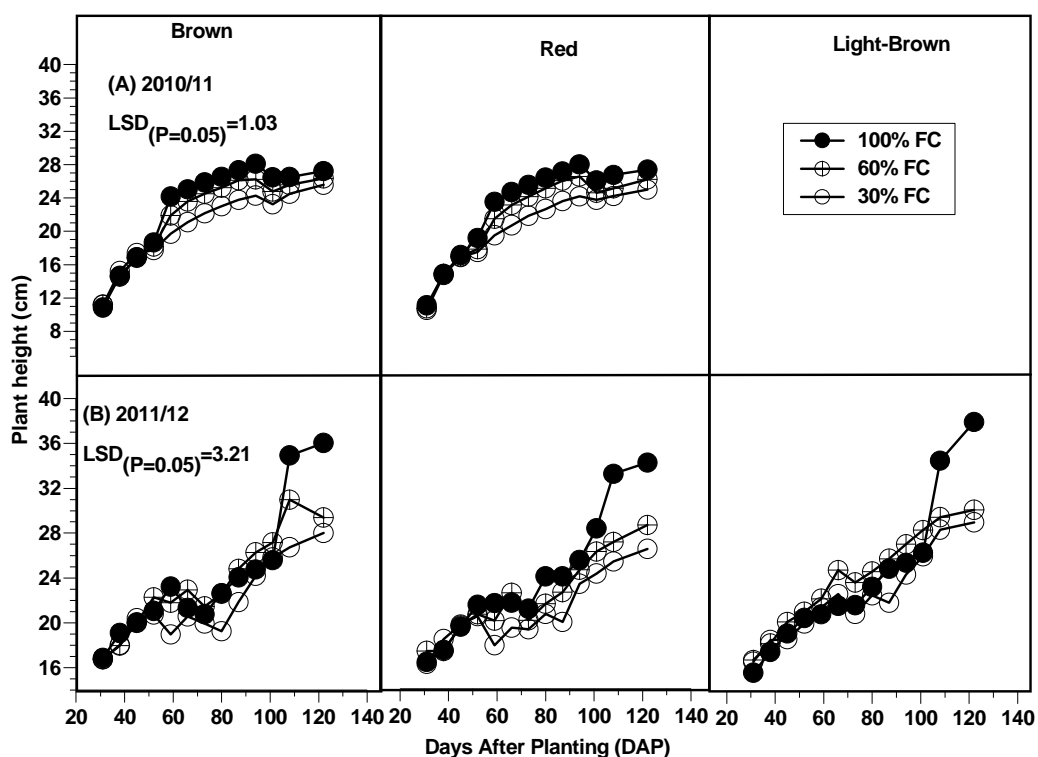


Figure 4: Plant height (cm) of bambara groundnut landraces ('Brown', 'Red' and 'Light brown') grown under a rainshelter during 2010/11 and 2011/12 planting seasons.

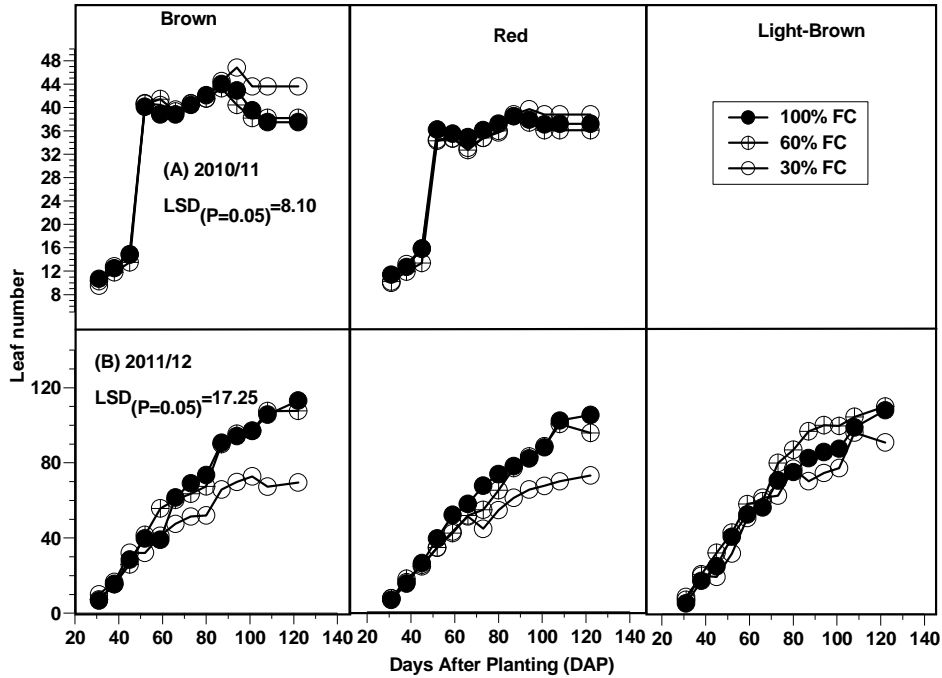


Figure 5: Leaf number of bambara groundnut landraces ('Brown', 'Red' and 'Light brown') grown under a rainshelter during 2010/11 and 2011/12 planting seasons.

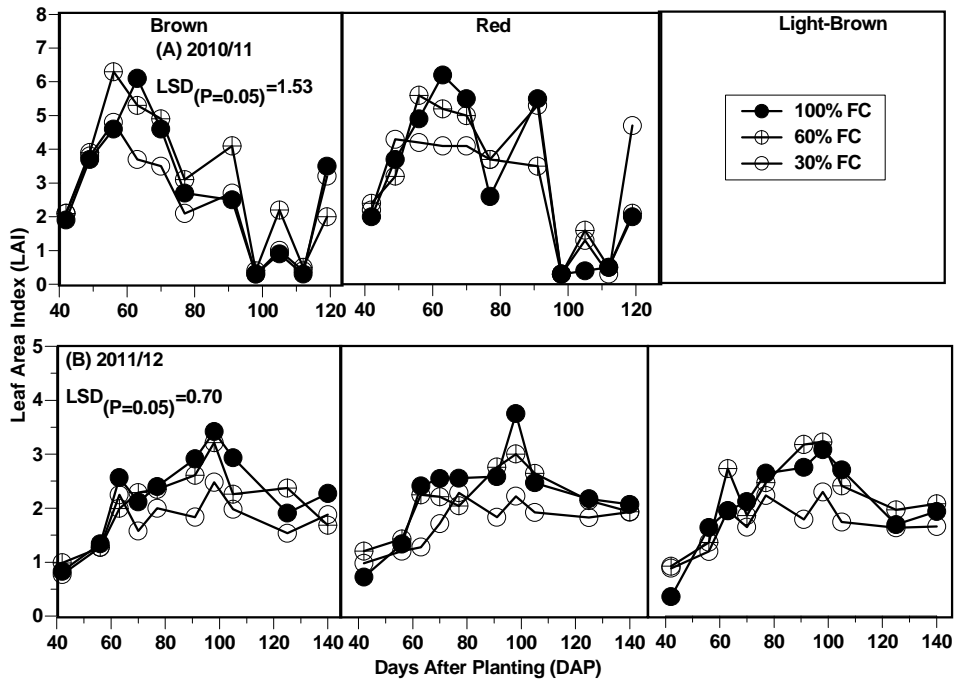


Figure 6: Leaf area index of bambara groundnut landraces ('Brown', 'Red' and 'Light brown') grown under a rainshelter during the 2010/11 and 2011/12 planting seasons.

With respect to LAI, for both seasons, there were no differences ( $P > 0.05$ ) between landraces, although the trend (2011/12) showed that 'Brown' and 'Red' performed better than 'Light-brown' (Figure 6). For both seasons, results showed a decrease in LAI in response to increasing water stress; LAI was lowest at 30% ETa compared with 60% and 100% ETa, respectively, which were statistically similar (Figure 6). The reduction in LAI in response to water stress was assumed to be due to a corresponding reduction in plant height and leaf number (Figures 4 & 5).

The growth responses of bambara groundnut to water stress have previously been described using similar growth indices of plant height, leaf number and leaf area index (Collinson et al., 1996, 1997, 1999; Mwale et al., 2007; Vurayai et al., 2011a, 2011b). There was consensus among the researchers that drought tolerance in bambara groundnut involved reduction in these growth indices. Reduced plant height, leaf number and LAI are mechanisms of reducing plant water use in response to decreasing soil water availability (Mitchell, 1998). Reduced canopy size is also responsible for increased water use-efficiency, although this often occurs at the expense of yield potential (Blum, 2005).

### ***Crop phenology***

Results of crop phenology were observed during the 2011/12 planting season when all three landraces were planted. With the exception of time to flowering, all other phenological stages showed highly significant differences ( $P < 0.001$ ) between water regimes but no differences ( $P > 0.05$ ) between landraces (Table 1). For all phenological events observed, mean separation showed that 60% and 100% ETa were statistically similar, but significantly different from 30% ETa (Table 1). Bambara groundnut landraces were shown to flower early, have a reduced flowering duration and mature early in response to decreasing soil water availability (Table 1). Water stress reduced the vegetative stage of bambara groundnut; landraces flowered earlier at 30% ETa compared with 60% and 100% ETa, respectively (Table 1).

**Table 1:** Phenological stages of bambara groundnut landraces ('Brown', 'Red' and 'Light-brown') in response to three water regimes (30%, 60% and 100% ETa) during 2011/12 planting season.

Water Regime ( <sup>x</sup> ETa)	Landrace	Flowering (DAP)	Flowering duration (Days)	Leaf senescence (DAP)	Maturity (DAP)
30%	Brown	61.00ab	35.00d	96.0b	119.8b
	Red	59.75b	42.00cd	101.8b	122.0b
	Light-brown	64.50ab	48.75abc	113.3a	126.5a
	<b>Mean</b>	<b>61.75<sup>b</sup></b>	<b>41.9<sup>b</sup></b>	<b>103.7<sup>b</sup></b>	<b>122.75<sup>b</sup></b>
60%	Brown	65.25ab	53.75ab	119.0a	128.0a
	Red	60.50ab	58.50a	119.0a	128.0a
	Light-brown	67.25a	46.00bc	113.2a	126.5a
	<b>Mean</b>	<b>64.33<sup>a</sup></b>	<b>52.8<sup>a</sup></b>	<b>117.1<sup>a</sup></b>	<b>127.50<sup>a</sup></b>
100%	Brown	65.75ab	53.25ab	119.0a	128.0a
	Red	65.25ab	53.75ab	119.0a	128.0a
	Light-brown	64.50ab	54.50ab	119.0a	128.0a
	<b>Mean</b>	<b>65.75<sup>a</sup></b>	<b>53.8<sup>a</sup></b>	<b>119.0<sup>a</sup></b>	<b>128.00<sup>a</sup></b>
LSD (P=0.05)	Water regime	3.73	5.72	5.52	1.74
LSD (P=0.05)	Landrace	3.73	5.72	5.52	1.74
LSD (P=0.05)	Water*Landrace	6.46	9.90	9.55	3.01

<sup>x</sup>ETa = crop water requirement. Values in the same column not sharing the same letter differ significantly at LSD (P=0.05). DAP = Days after planting.

Since bambara groundnut landraces took long to establish (Figure 1), this effectively resulted in a shortened vegetative period which may also be linked to reduced plant height and leaf number under water limited conditions (Figures 4 & 5). In addition, water stress reduced the reproductive stage; decreased water availability resulted in shortened flowering duration or reproductive period at 30% ETa compared with 60% and 100% ETa, respectively (Table 1). Furthermore, water stress reduced the overall length of bambara groundnut landraces' crop cycle through early leaf senescence and subsequently early maturity (Table 1). With respect to landraces, 'Brown' and 'Red' landraces showed a consistent trend in flowering and maturing early in response to limited water availability compared with 'Light-brown'. However, 'Red' had a longer reproductive period compared with 'Brown' and 'Light-brown', respectively; this was due to delayed leaf senescence in the 'Red' landrace (Table 1).

Early flowering, due to reduced vegetative growth (leaf number and area) is a major mechanism for moderating water loss under drought stress (Blum, 2005). According to Araus



et al. (2002), early flowering in response to limited water availability, is a drought escape mechanism. This is equally true for reduced flowering duration, with the objective being to reproduce before water stress becomes terminal. Selection for high water use efficiency under limited water supply has tended to be biased towards plants that flower early and maintain a smaller canopy size (Blum, 2005, 2009). Hence, by definition, bambara groundnut landraces may be suitable for production under dryland conditions that require plants with a small canopy, moderated growth and short growth duration under water limited conditions.

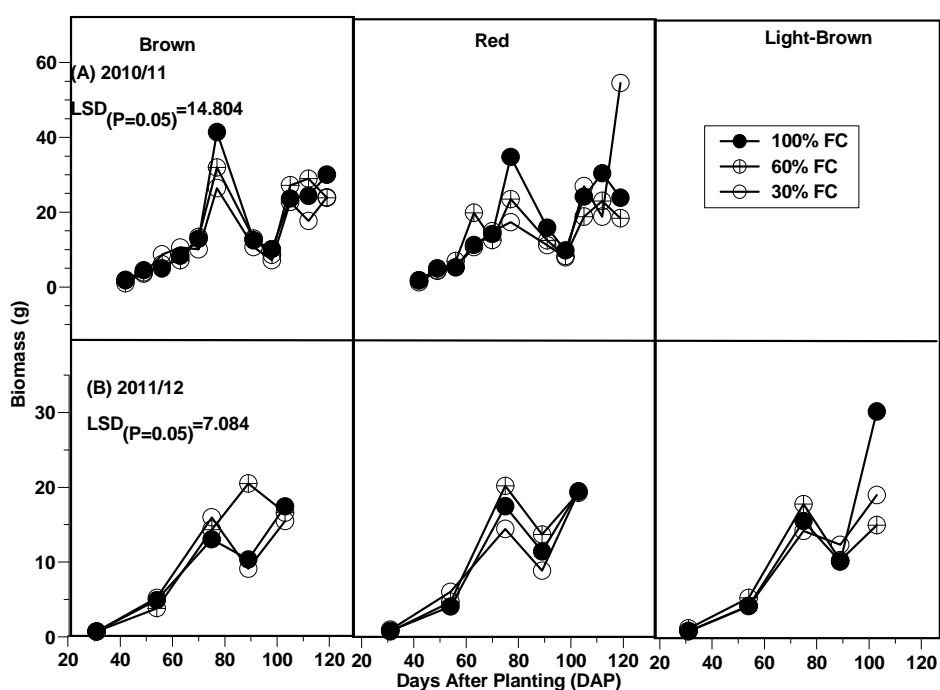


Figure 7: Biomass accumulation (per plant per dry matter basis) of bambara groundnut landraces ('Brown', 'Red' and 'Light brown') grown under a rainshelter during the 2010/11 and 2011/12 planting seasons.

### *Biomass, Yield and Water Use*

Biomass accumulation, over time, for both seasons, showed no significant differences ( $P > 0.05$ ) between water regimes as well as between landraces (Figure 7). However, closer inspection of results showed a trend of biomass decreasing with increasing water stress (Figure 7); although there was variability between landraces. During 2010/11, this observation was clear at 112 DAP, which also corresponded with the vegetative peak of the plants (Figure 7).

**Table 2:** Yield components of bambara groundnut landraces ('Brown' and 'Red') in response to three water regimes (30%, 60% and 100% ETa) during 2010/11 season.

<b>Water Regime</b> ( <sup>x</sup> ETa)	<b>Landrace</b>	<b>HI*</b> (%)	<b>Pod Mass (g)</b>	<b><sup>x</sup>Pod No.</b> (plant <sup>-1</sup> )	<b>Biomass</b> (t.ha <sup>-1</sup> )	<b>Yield</b> (t.ha <sup>-1</sup> )	<b><sup>y</sup>WUE</b> (kg.m <sup>-3</sup> )
<b>30%</b>	Brown	10.55c	2.293b	2b	3.259a	0.114c	0.262a
	Red	15.04bc	1.900b	3b	2.315a	0.215bc	0.186a
	<b>Mean</b>	<b>12.80<sup>c</sup></b>	<b>2.10<sup>c</sup></b>	<b>3<sup>c</sup></b>	<b>2.79<sup>b</sup></b>	<b>0.16<sup>b</sup></b>	<b>0.224<sup>a</sup></b>
<b>60%</b>	Brown	18.39bc	3.893b	8b	4.176a	1.078bc	0.255a
	Red	14.65bc	3.180b	7b	3.886a	1.125b	0.237a
	<b>Mean</b>	<b>16.50<sup>bc</sup></b>	<b>3.54<sup>b</sup></b>	<b>7<sup>b</sup></b>	<b>4.03<sup>a</sup></b>	<b>1.10<sup>b</sup></b>	<b>0.246<sup>a</sup></b>
<b>100%</b>	Brown	51.83a	8.883a	17a	3.062a	2.701a	0.139a
	Red	27.12b	7.712a	15a	5.011a	2.486a	0.233a
	<b>Mean</b>	<b>39.30<sup>a</sup></b>	<b>8.30<sup>a</sup></b>	<b>16<sup>a</sup></b>	<b>4.04<sup>a</sup></b>	<b>2.59<sup>a</sup></b>	<b>0.186<sup>a</sup></b>
Yield correlation (r)		0.295	0.649	0.869	0.943	-----	-----
LSD <sub>(P=0.05)</sub> Water regime		10.48	1.946	4	1.906	0.652	0.116
LSD <sub>(P=0.05)</sub> Landrace		8.55	1.589	4	1.556	0.533	0.095
LSD <sub>(P=0.05)</sub> Land*Treat		14.82	2.752	6	2.696	0.923	0.164

<sup>x</sup>ETa = crop water requirement. \*HI = harvest index; <sup>x</sup>Pod number values were rounded off to the nearest integer since pod number represents discrete data; <sup>y</sup>WUE = water use efficiency. Values in the same column not sharing the same letter differ significantly at LSD (P=0.05).

**Table 3:** Yield components of bambara groundnut landraces ('Brown', 'Red' and 'Light-brown') in response to three water regimes (30%, 60% and 100% ETa) during 2011/12 planting season.

Water Regime (xETa)	Landrace	HI* (%)	xPod			Yield (t.ha <sup>-1</sup> )	yWUE (kg.m <sup>-3</sup> )
			Pod Mass (g)	No. (plant <sup>-1</sup> )	Biomass (t.ha <sup>-1</sup> )		
30%	Brown	15.7a 12.26a	4.914bc	7ab	5.414c	0.362b	0.114ab
	Red	b 14.39a	5.361bc	8ab	7.414bc	0.348b	0.144a
	Light-brown	b	6.446bc	10ab	7.856abc	0.652ab	0.093b
	<b>Mean</b>	<b>14.02<sup>a</sup></b>	<b>5.57<sup>a</sup></b>	<b>8.46<sup>a</sup></b>	<b>6.91<sup>b</sup></b>	<b>0.45<sup>a</sup></b>	<b>0.120<sup>a</sup></b>
60%	Brown	12.30a b 11.63a	6.015bc	8ab	8.550abc	0.623ab	0.096b
	Red	b 15.34a	6.084bc	8ab	8.612abc	0.319b	0.118ab
	Light-brown	b	8.761ab	11ab	9.468ab	0.712ab	0.129ab
	<b>Mean</b>	<b>13.09<sup>a</sup></b>	<b>6.95<sup>a</sup></b>	<b>9.02<sup>a</sup></b>	<b>8.88<sup>ab</sup></b>	<b>0.55<sup>a</sup></b>	<b>0.110<sup>ab</sup></b>
100%	Brown	7.82b	4.214c	5ab	8.757abc	0.419b	0.110ab
	Red	9.81ab	4.549bc	7ab	8.107abc	0.518b	0.097b
	Light-brown	15.99a	10.699a	13a	11.054a	1.013a	0.107ab
	<b>Mean</b>	<b>11.21<sup>a</sup></b>	<b>6.49<sup>a</sup></b>	<b>8.49<sup>a</sup></b>	<b>9.31<sup>a</sup></b>	<b>0.65<sup>a</sup></b>	<b>0.100<sup>b</sup></b>
Yield correlation (r)		0.541	0.592	0.853	0.697	-----	-----
LSD <sub>(P=0.05)</sub> Water regime		3.938	2.188	3.645	1.715	0.214	0.021
LSD <sub>(P=0.05)</sub> Landrace		3.938	2.188	3.645	1.715	0.214	0.021
LSD <sub>(P=0.05)</sub> Land*Water		6.821	3.790	6.313	2.970	0.370	0.037

<sup>x</sup>ETa = crop water requirement. \*HI = harvest index; <sup>x</sup>Pod number values were rounded off to the nearest integer since pod number represents discrete data; <sup>y</sup>WUE = water use efficiency. Values in the same column not sharing the same letter differ significantly at LSD (P=0.05).

Crop yield during 2010/11 showed a clearer trend, with regards to differences between water regimes (Table 2). With the exception of final biomass, all other parameters measured showed highly significant differences (P < 0.001) between water regimes; there were no differences (P > 0.05) between the two landraces ('Brown' and 'Red') for all yield components. The results showed a trend of decline in HI, pod mass, pod number, biomass and grain yield in response to water stress. Correlations of the data showed that HI (r = 0.649), pod

mass ( $r = 0.869$ ) and pod number ( $r = 0.943$ ) contributed significantly to yield. Consequently, reduction in yield under stress was due to decreased HI, pod mass and number (Table 2).

Yield results from 2011/12 were contrary to the trend observed during 2010/11 (Table 3). With the exception of biomass, all other yield components showed no differences ( $P > 0.05$ ) between landraces and water regimes; there was also no clear trend in response to water stress. Only final biomass was significantly ( $P < 0.05$ ) affected by water stress, with biomass decreasing in response to 60% ETa and 30% ETa, respectively (Table 3). Yields achieved during the 2011/12 planting season were also significantly lower than yields achieved in the previous season. Although correlations showed a similar trend as in the previous season, they were lower than those reported for 2010/11; suggesting overall poor crop performance during 2011/12.

Results of yield, for both planting seasons, showed that pod yield (pod number and mass) was the greatest influence to seed mass or yield. Even though bambara groundnut has been reported to be drought tolerant, water stress was still able to affect yield. These results are similar to other reports in the literature (e.g. Babiker, 1989; Berchie et al., 2010; Berchie et al., 2012) who all reported reduced seed yield in bambara groundnut landraces in response to limited water availability. In this study, reduced seed yield, through reduced pod mass and number, may be related to a shorter flowering duration, which limited pod number, while low pod mass may be linked to earlier senescence which affected pod filling. This was also observed in the number of empty pods. However, what is noteworthy is bambara groundnut's ability to still produce yield even under severe water stress (30 % ETa). According to Berchie et al. (2012), this confirms bambara groundnut's resilience under drought stress and further justifies the need for more research on the crop, with a view to promoting it as a food security crop.

Results of water use efficiency (WUE) showed no (significant) differences ( $P > 0.05$ ) between water regimes as well as between landraces for both planting seasons (Tables 2 & 3). During the 2010/11 planting season, WUE was highest at 60% and 30% ETa, respectively, compared with 100% ETa, suggesting that WUE increased in response to limited water availability. The lack of clear differences between treatments during 2010/11 was due to the numerator – biomass, which also showed a trend of no differences between treatments (Table

2). However, during the 2011/12 planting season, the observed trend showed WUE increasing with decreasing water availability. Water use efficiency was highest in the 30% ETa treatment, followed by 60% and 100%, respectively; mean separation showed that WUE at 30% ETa was significantly higher than at 100% ETa but similar to the 60% ETa water regime. This was in line with the trend observed for final biomass during the 2011/12 season (Table 3), suggesting that WUE was more influenced by biomass than water use.

High water use efficiency under limited water conditions is linked to reduced canopy size (plant height, leaf number, LAI), reduced transpirational losses (low stomatal conductance) as well as a shortened growth duration (Blum, 2005, 2009). While reduced canopy size and stomatal closure directly moderate water losses by the crop, reduced crop duration effectively reduces the amount of water applied to the crop. As such, in line with observed reductions in canopy size, stomatal conductance and crop duration, WUE increased in response to declining water availability. Our results of WUE, although slightly higher, were similar to those reported in a long running project on bambara groundnut (BAMFOOD), where it was found bambara groundnut's WUE is about  $2.1 \text{ g mm}^{-1} \text{ m}^{-2}$ , a value which was comparable to that of other legumes (Azam-Ali et al., 2004). However, as argued by Blum (2005, 2009), increased WUE often occurs at the expense of yield potential.

## **Conclusions**

This study showed that bambara groundnut landraces have some resilience to reduced water availability. Increased water use efficiency in bambara groundnut landraces in response to water stress was achieved through canopy size and crop duration adjustments. Limited water availability resulted in reduction in growth indices of plant height, leaf number and leaf area index, thus minimising water losses. In addition, bambara groundnut landraces were shown to respond to limited water availability through closure of stomata, thus reducing transpirational losses. Furthermore, imposition of stress resulted in early flowering, reduced flowering duration, early senescence and ultimately, early maturity. These responses are characteristic of drought avoidance and escape mechanisms. Water stress was shown to reduce seed yield through reduced pod number and mass, although bambara groundnut landraces were shown to be still productive under limited water conditions. While bambara groundnut landraces showed growth and phenological responses to water stress, slow establishment in bambara groundnut landraces may result in water losses through soil evaporation during the establishment stage. Lastly, although there was much variability between 'Brown', 'Light-brown' and 'Red' landraces, the trend showed that the darker colours were more consistent in their responses to water stress.

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## **References**

**(See final reference list pages 198-228)**

## CHAPTER 7

### **Intercropping taro and bambara groundnut landraces under dryland conditions in KwaZulu-Natal, South Africa**

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## **Abstract**

Despite its high nutritional value, bambara groundnut (*Vigna subterranea*) has lost popularity amongst rural farmers of KwaZulu-Natal, South Africa, while taro (*Colocasia esculenta*) has improved in status due to recently improved access to markets. Intercropping taro and bambara groundnut may offer farmers an opportunity to mimic historical diversity that existed in traditional agro-ecosystems. This study aimed at evaluating productivity of a taro - bambara groundnut intercrop under rainfed conditions. Trials were planted over two summer seasons, 2010/11 and 2011/12, in rural areas of KwaZulu-Natal. Treatments included taro and bambara groundnut sole crops as well as 1:1 (taro:bambara groundnut) and 1:2 intercrops. Growth and yield parameters were determined for each crop. Land equivalent ratio (LER) was calculated to evaluate intercrop productivity. Plant height of taro, the main crop, was not affected by intercropping in both seasons. Taro leaf number was negatively affected ( $P < 0.001$ ) by intercropping resulting in reduced leaf number compared with sole cropping. Increasing the proportion of bambara groundnut in the intercrop significantly decreased taro leaf number in the 1:2 intercrop relative to the 1:1 intercrop. However, growth of bambara groundnut responded positively ( $P < 0.05$ ) to intercropping in that plants were taller and had more leaves. Although yield generally decreased under intercropping compared with sole cropping, it was shown that, taro and bambara groundnut yields were not significantly affected by intercropping. LER showed that intercropping taro was more productive than sole cropping. On average, the 1:1 and 1:2 intercrops had LERs of 1.53 and 1.23, respectively. Intercropping taro and bambara groundnut at a ratio of 1:1 is feasible and productive under rainfed conditions.

**Keywords:** Growth, land equivalent ratio (LER), productivity, yield



## 1 Introduction

A growing niche market for organically produced eddoe type taro (*Colocasia esculenta* L. Schott) has recently emerged in South Africa (Modi, 2003). This has resulted in an increase in taro production, in terms of area of land under cultivation and numbers of subsistence farmers cultivating it in pure stands. Most of these farmers are women, who now depend on the income received from marketing the crop to retail chains as a source of livelihood (Eybers, 2008). However, increased taro cultivation, as a sole crop, has led to a possible loss in species diversity, thus it could expose farmers to food and nutrition insecurity in the event of crop failure. This has resulted in a shift from traditional cropping systems, which have historically been diverse and shown to be effective in safe guarding rural household food security (Azam-Ali, 2010). One such crop species in danger of being forgotten is bambara groundnut (*Vigna subterranea* L. Verdc), an underutilized crop whose production has declined drastically over the years.

Although bambara groundnut, a legume with much potential for bolstering food security, has been reported to be drought tolerant (Linnemann and Azam-Ali, 1993), its cultivation in pure stands remains relatively uncommon. Similar to taro, it too is preserved mostly women by (Mukurumbira, 1985) who intercrop it with crops such as maize, millet, sorghum, cassava, yam, peanut and cowpea (Karikari, 2003). Globally, focus has been shifting to research on neglected underutilized species, as possible future food security crops. This could be because the cropping systems in which they are cultivated and the people who manage, protect and consume them represent elements of agro-biodiversity (Azam-Ali, 2010). Additionally, the fact that climate change is underway (Hassan, 2006) has emphasized the need for identifying resilient crops and farming systems. Intercropping taro and bambara groundnut may offer farmers the opportunity to mimic this historical diversity.

According to a recent review by Lebot (2009), in the Asia-Pacific, intercropping of taro in rainfed agroforestry systems is a widespread practice. There are few reports in literature highlighting successful intercropping of taro with several crops; black pepper (*Piper nigrum*) (Silbanus and Raynor, 1993), alfalfa, sweet corn, peanut, sweet potato and sugar bush (De la Peña and Melchor, 1993), and a legume, *Crotalaria juncea* (Silva *et al.*, 2008). In these instances, results showed that intercropping had no effect on corm yield of taro. Local farmers

in KwaZulu-Natal, South Africa who also rely on rainfed farming no longer practice intercropping. Furthermore, there is no information describing intercropping of local taro landraces.

While taro, a starchy crop, is reported to be not very drought tolerant and a heavy feeder of nutrients, especially nitrogen due to its large leaves (Lebot, 2009), bambara groundnut, on the other hand, is said to be drought tolerant (Linnemann and Azam-Ali, 1993) and is also a legume with ability to fix atmospheric nitrogen. Inclusion of legumes in intercrops also boosts the dietary nutrients produced per unit area of land (Mukhala *et al.*, 1999). As such, intercropping taro and bambara groundnut may be beneficial with regards to crop diversification, strengthening household food security and sustainability of agriculture. Therefore, in this study, it was hypothesized that farmers already growing taro could intercrop it with bambara groundnut without risking yield losses to their taro and that intercropping taro and bambara groundnut would be more productive than growing either one of them in pure stands.

## **2 Materials and methods**

### *2.1 Planting material*

A taro landrace was obtained from subsistence farmers in the Umbumbulu rural district (29°36'S; 30°25'E) in KwaZulu-Natal, South Africa. The landrace was classified as an eddoe type of taro, characterized by a central corm and numerous side cormels. Seeds of a bambara groundnut landrace were collected from subsistence farmers in Jozini (27°26'S; 32°4'E), northern KwaZulu-Natal, South Africa. The bambara groundnut landrace was characterized according to seed coat colour (Sinefu, 2011) and thereafter the “Red” landrace was used in this study.

## *2.2 Site description*

The trials were planted at a homestead in Umbumbulu (29°36'S; 30°25'E), located in the midlands of KwaZulu-Natal, over two summer seasons (2010/11 and 2011/12) under dryland conditions. The soils at the trial site were classified as sandy clay loam (USDA Classification). The field chosen for the trials had been previously fallow for two seasons.

## *2.3 Experimental design*

The experimental design was a factorial experiment, arranged in a completely randomized block design, replicated three times. The component crops were taro and bambara groundnut. The intercropping style used in the study was row-intercropping whereby both crops were planted simultaneously. Treatments included taro and bambara groundnut sole crops each, and two intercrop combinations. The intercrop combinations were 1:1 (taro: bambara groundnut) and 1:2. Plant spacing for taro was 1 m between rows x 0.5 m within rows. Within-row spacing for bambara groundnut was 0.3 m.

## *2.4 Agronomic practices*

Soil samples were taken for soil fertility and textural analysis prior to planting. Land preparation was done by hand-hoeing to a depth of 60 cm. Based on soil fertility results, an organic fertilizer, Gromor Accelerator® (Mare, 2010), was applied at planting. Routine weeding and ridging of both taro and bambara groundnut were done using hand-hoes.

## *2.5 Data collection and analyses*

Data collection, for both seasons, was done every 10 days to determine plant growth parameters of height and leaf number. At harvest, biomass (B), yield (Y), yield components and harvest index (HI) for each crop were determined. Productivity of the intercrop was evaluated using the Land Equivalent Ratio (LER) as described by Willey (1979);

$$LER = L_A + L_B = \frac{Y_A}{S_A} + \frac{Y_B}{S_B} \quad \text{Equation 1}$$

Where  $L_A$  and  $L_B$  are the partial LERs of taro and bambara groundnut, respectively,  $Y_A$  and  $Y_B$  are the intercrop yields of taro and bambara groundnut, respectively, and  $S_A$  and  $S_B$  are their respective sole crop yields.

Weather parameters for the duration of the trials were monitored and data collected from an automatic weather station located at the homestead (Table 1). Soil water content was also monitored using a PR2/6 profile probe operated with an HH2 handheld moisture meter (Delta-T Devices, UK).

Data were analyzed using the analysis of variance (ANOVA) algorithm in GenStat<sup>®</sup> (Version 14, VSN International Ltd, UK). Duncan's Multiple Range Test (DMRT) was used for mean separation at the 5% level of significance.

### 3 Results

#### 3.1 Taro growth

There was variability in the amount of rainfall received in the two seasons with regards to rainfall distribution during the season (Table 1). This may, in part, explain the negative trend of declining leaf number observed during 2010/11 season. Results showed that for all treatments in 2010/11, leaf number declined from the point of initial measurement (Fig 1). Data collection may have coincided with mid-season drought in the later part of January and February (Table 1) resulting in taro continuously shedding leaves.

For both seasons, taro growth (plant height and leaf number) was negatively affected ( $P < 0.05$ ) by intercropping (Fig 1). Increasing the proportion/rows of bambara groundnut in the intercrop resulted in lower plant height and leaf number for taro comparing the 1:1 and 1:2 intercrops to the sole crop. However, despite this decrease, plant height in the sole crop was

statistically similar to the 1:1 intercrop. Results of leaf number, for both seasons, showed a similar trend as that observed for plant height; sole cropping produced the most leaves compared with the 1:1 and 1:2 intercrops (Fig 1).

Table 1. Rainfall (monthly and season total) and mean temperature data for Umbumbulu, KwaZulu-Natal, South Africa.

		Total	Oct	Nov	Dec	Jan	Feb	Mar	April	May
<b>Rainfall</b> (mm)	<b>2010/11</b>	894	97.4	168.2	192.2	165.2	81.8	73.4	71.2	39.6
	<b>2011/12</b>	648.8	28.2	144.2	72.8	85.8	162.4	75.6	55.6	24.2
<b>Mean</b> <b>Temp (°C)</b>	<b>2010/11</b>		18.7	19.7	19.6	21.2	22.3	20.9	19.0	18.6
	<b>2011/12</b>		17.3	17.6	20.7	23.3	23.5	20.6	18.3	17.2

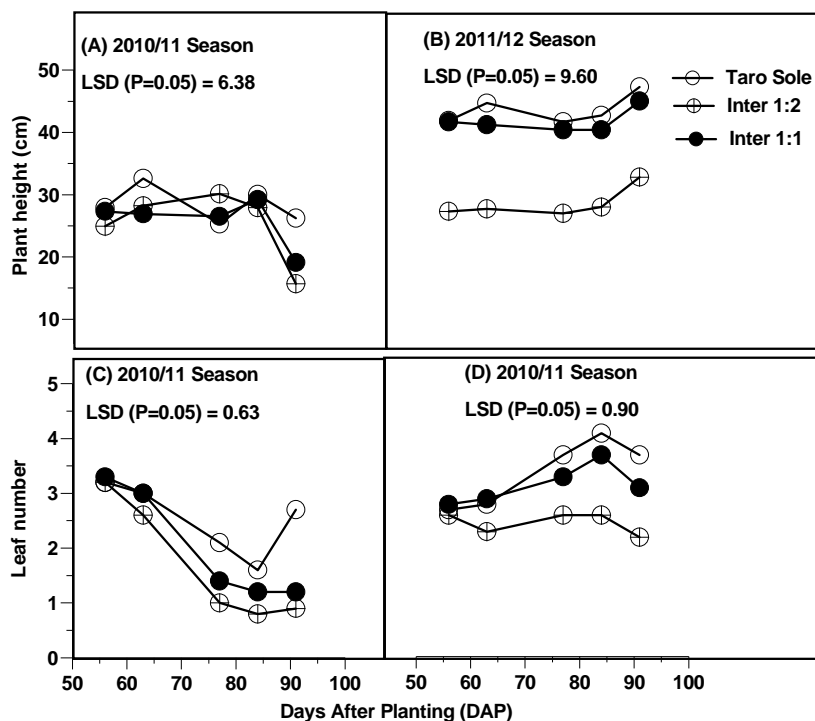


Figure 1: Comparisons of plant height and leaf number of taro grown under sole cropping, 1:1 and 1:2 intercropping grown during 2010/11 and 2011/12 planting season.

### *3.2 Bambara groundnut growth*

It was observed that intercropping had variable effects on growth of bambara groundnut. During the 2010/11 season, increasing the proportion of bambara groundnut increased plant height and leaf number (Fig 2). Intercropping had a positive effect ( $P < 0.001$ ) on plant height and leaf number of bambara groundnut; plants in the 1:1 and 1:2 intercrops were taller and had more leaves compared with the sole crop (Fig 2).

In line with the trend for plant height established in the first season, no significant difference ( $P > 0.05$ ) was found in plant height between the sole crop and two intercrops during the 2011/12 season (Fig 2). Intercropping bambara groundnut at a ratio of 1:1 resulted in taller plants compared with sole cropping and intercropping at a ratio of 1:2 (Fig 2). Contrary to the previous season's findings, intercropping resulted in significantly ( $P < 0.001$ ) fewer leaves compared with sole cropping.

### *3.3 Yield*

With respect to statistical differences, intercropping had no significant effect ( $P > 0.05$ ) on harvest index (HI) across either season (2010/11 and 2011/12). The trend was that during the 2010/11 season, the sole crop had the highest HI relative to the 1:1 and 1:2 intercrops respectively, while during the 2011/12 season, the 1:1 intercrop performed better than the sole crop and 1:2 intercrop, respectively (Table 2). Results of HI were consistent with reduced canopy size (plant height and leaf number) observed under intercropping. This observation was clearer in the 1:2 intercrop.

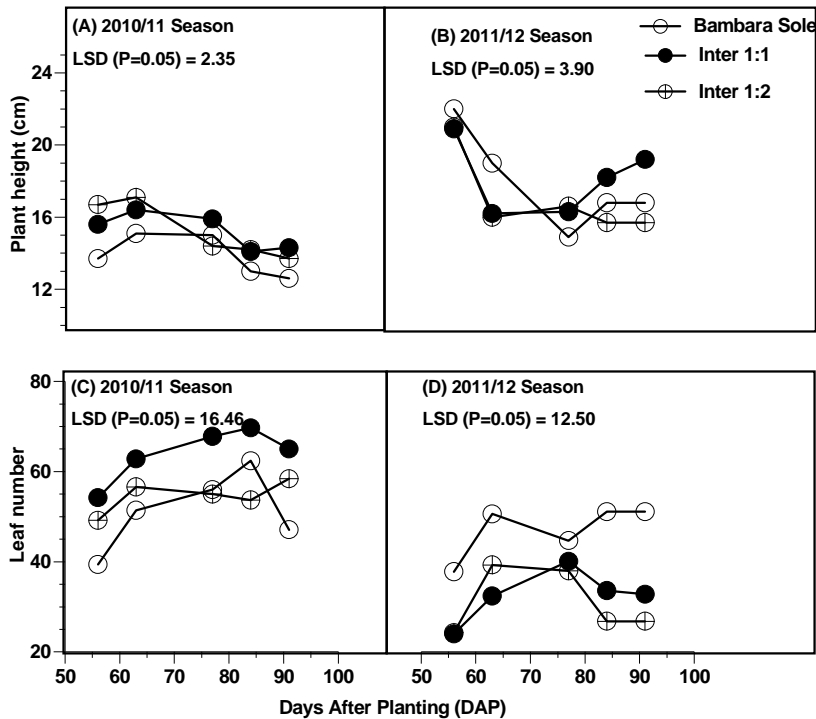


Figure 2: Comparisons of plant height and leaf number of bambara groundnut grown under sole cropping, 1:1 and 1:2 intercropping grown during 2010/11 and 2011/12 planting season.

In addition, intercropping was shown not to significantly affect ( $P > 0.05$ ) corm number per plant during both planting seasons (Table 2). The trend, for both seasons, showed that intercropping at a ratio of 1:1 resulted in the highest corm number per plant compared with sole cropping and intercropping at a ratio of 1:2, respectively. This was consistent with observations of HI, especially during the second planting season (Table 2).

Consistent with the results of corm number per plant, it was also shown that, for both seasons, intercropping had no significant effect ( $P > 0.05$ ) on final yield ( $t\ ha^{-1}$ ) of taro (Table 2). Despite lack of statistical differences this study showed that sole cropping consistently produced higher than intercropping at ratios of 1:1 and 1:2, respectively. This was despite the 1:1 intercrop having higher corm number per plant than the sole crop suggesting that intercropping may have resulted in more but smaller sized corms compared with sole cropping.

Table 2. Yield and productivity of a taro - bambara groundnut intercrop under dryland conditions. <sup>w</sup>HI = harvest index; <sup>x</sup>CMN = corm number per plant; <sup>y</sup>PDN = pod number per plant; <sup>z</sup>LER = land equivalent ratio. \*Values were rounded off to the nearest whole number since CMN and PDN are discrete values. Numbers with different letters in the same column differ statistically at the 5% level of significance.

Season	Intercrop	Taro			Bambara groundnut			
		HI <sup>w</sup>	*CMN <sup>x</sup> (plant <sup>-1</sup> )	Yield (t ha <sup>-1</sup> )	HI <sup>w</sup>	*PDN <sup>y</sup> (plant <sup>-1</sup> )	Yield (t ha <sup>-1</sup> )	LER <sup>z</sup>
2010/11	Sole Crop	0.83a	7a	6.29ab	0.46ab	14a	0.34ab	-----
	1:1	0.76ab	6a	5.03ab	0.52a	22a	0.31ab	1.71a
	1:2	0.73ab	6a	4.55ab	0.33abc	16a	0.22b	1.36b
	Mean	<b>0.77<sup>a</sup></b>	<b>6.41<sup>a</sup></b>	<b>5.29<sup>a</sup></b>	<b>0.44<sup>a</sup></b>	<b>17.00<sup>a</sup></b>	<b>0.29<sup>b</sup></b>	<b>1.54<sup>a</sup></b>
2011/12	Sole Crop	0.77ab	5a	6.98a	0.20c	27a	0.97a	-----
	1:1	0.80ab	7a	5.66ab	0.24bc	26a	0.51ab	1.34b
	1:2	0.69b	4a	3.88b	0.27abc	20a	0.53ab	1.10b
	Mean	<b>0.76<sup>a</sup></b>	<b>5.41<sup>a</sup></b>	<b>5.51<sup>a</sup></b>	<b>0.24<sup>b</sup></b>	<b>24.19<sup>a</sup></b>	<b>0.67<sup>a</sup></b>	<b>1.23<sup>b</sup></b>
<b>LSD<sub>(P=0.05)</sub> (Intercrop)</b>		<b>0.07</b>	<b>2.05</b>	<b>1.82</b>	<b>0.17</b>	<b>10.59</b>	<b>0.44</b>	<b>0.217</b>
<b>LSD<sub>(P=0.05)</sub> (Season)</b>		<b>0.06</b>	<b>1.68</b>	<b>1.48</b>	<b>0.14</b>	<b>8.65</b>	<b>0.36</b>	<b>0.217</b>
<b>LSD<sub>(P=0.05)</sub> (Int*Season)</b>		<b>0.10</b>	<b>2.91</b>	<b>2.57</b>	<b>0.24</b>	<b>14.98</b>	<b>0.62</b>	<b>0.307</b>

Yield results (t ha<sup>-1</sup>) for bambara groundnut showed no significant differences (P > 0.05) between sole cropping and intercropping at ratios of 1:1 and 1:2 during both seasons. However, the trend showed that yield was highest in the sole crop relative to the 1:1 and 1:2 intercrops, respectively (Table 2). Intercropping at a ratio of 1:2 consistently produced the least yield, especially during the 2010/11 season. A comparison of yield between the two planting seasons showed that higher yields were achieved during 2011/12 compared with 2010/11 (Table 2). This was despite 2011/12 receiving less rainfall than 2010/11 (Table 1).



### 3.4 Intercrop productivity

Intercrop productivity was evaluated using the LER. During 2010/11, there were significant differences ( $P < 0.001$ ) between the 1:1 and 1:2 intercrops for LER (Table 2). Intercropping at a ratio of 1:1 was shown to be more productive with an LER of 1.71 compared with 1.36 for the 1:2 intercrop. During the subsequent season (2011/12), there were no differences ( $P > 0.05$ ) between the intercrops, although LER remained higher for the 1:1 compared with the 1:2 intercrop. Over both seasons, intercropping taro with bambara groundnut was shown to be more productive than growing either of the two crops as sole crops (Table 2).

## 4 Discussion

From as early as the 1970s, a growing interest in intercropping had been noted (Willey, 1979). Such interest was driven by the potential intercropping had, with respect to improving resource utilisation and overall productivity of cropping systems. However, to date, more still needs to be done in terms of intercropping and crop combinations. Previous efforts have focused on evaluating cereal-legume intercrops (Reinhardt and Tesfamichael, 2011) due to the beneficial effects. Limited research has been conducted on intercropping neglected underutilized species (NUS) which remain a feature of rural production systems. Intercropping NUS such as taro and bambara groundnut may improve resilience of the current cropping system in rural areas of KwaZulu-Natal since bambara groundnut has been reported to be drought tolerant (Linnemann and Azam-Ali, 1993). In this study, we evaluated the productivity of a taro – bambara groundnut intercrop under dryland conditions.

Results of this study showed that, to a limited extent, intercropping taro with bambara groundnut had a negative effect on taro growth, specifically leaf number. While there was no negative effect on plant height of taro, increasing the proportion of bambara groundnut in the intercrop resulted in reduced leaf number. Contrary to our findings, Silva *et al.* (2008) observed taller plants and no changes to leaf area when intercropping taro with a legume *Crotalaria juncea*. Karikari (2003) previously reported that intercrops with a proportion of bambara groundnut greater than 50% were less productive for the other component crop.

Another factor that may have affected taro growth was rainfall distribution. Uneven rainfall distribution during the 2010/11 season, possibly resulting in intermittent drought, may have accounted for the trend of declining growth observed in taro. Furthermore, the results of the present study may have been due to increased inter-species competition for resources such as water and nutrients. However, bambara groundnut is reported to have a deep root system (Swanevelde, 1998) compared with the shallow fibrous roots found in taro (Lebot, 2009). This would imply that the two crops can co-exist since they can access water from different levels of the soil profile. In this study, it was shown that intercropping taro and bambara groundnut at a ratio of 1:1 resulted in growth that was statistically similar to that observed under sole cropping.

Intercropping taro with bambara groundnut was shown to have no significant negative effect on yield components and final yield of taro across both seasons. While sole cropping generally performed better than the two intercrop combinations, results showed that, for certain yield components such as harvest index and corm number, the 1:1 intercrop often performed better than the sole crop and 1:2 intercrop. The trend of HI was consistent with observations of plant growth showing reduction in leaf number and plant height. Improved HI in the 1:1 intercrop observed in the second season gives credence to the benefit of intercropping two crops with different maturity dates as reported by Fukai and Trenbath (1993). These authors suggested that reduced vegetative growth would leave plants with enough assimilate later in the season for partitioning to the harvestable parts.

There are various benefits of intercropping taro with legumes (de la Peña and Melchor, 1993) one of which is yield stability (Willey, 1979). Although taro yields were lower than those reported by de la Peña and Melchor (1993), our results were similar with their observations that there were no significant differences between treatments. Silva *et al.* (2008) also reported that intercropping had no effect on taro yield. Here we showed that intercropping taro with bambara groundnut at a ratio of 1:1 had negligible effect on corm yield of taro suggesting that farmers would not face a loss in possible income if they were to intercrop.

Although sole cropping yielded higher than intercropping at ratios of 1:1 and 1:2, respectively, the 1:1 intercrop had higher corm number per plant than the sole crop. This suggests that intercropping may have resulted in more but smaller sized corms compared with

sole cropping. This is in line with the sole crop having a larger canopy relative to the intercrops, thereby implying a greater source size capable of partitioning more assimilate to the corms (sink). Reduced canopy size in the 1:1 and 1:2 intercrops may have resulted in a smaller source, while the increased corm number per plant meant a larger sink thus resulting in less assimilate being partitioned to the numerous corms.

According to Willey (1979), one criterion for intercropping is to evaluate if intercropping a main crop with another crop will not affect yield of the main crop. Under this objective, it may be assumed that any yield obtained from the second crop will be acceptable to the farmer (Willey, 1979). In the present case, we sought to evaluate whether intercropping taro with bambara groundnut would not affect yield of taro, which the farmers rely on as a cash crop, hence any yield of bambara groundnut achieved would be deemed an acceptable bonus. It is important to note that, for all cases, our yields of bambara groundnut achieved in the intercrops were comparable to results of bambara groundnut recorded in experiments where bambara groundnut was grown in pure stands (Sinefu, 2011). Previous reports (Karikari, 2003) have been to the contrary suggesting that bambara groundnut intercropping systems were less productive than sole crops of their component crops. In the current study we were able to show that intercropping taro with bambara groundnut at a ratio of 1:1 would not affect taro yield, but also offer farmers decent yields of bambara groundnut for their dietary requirements.

The Land Equivalent Ratio (LER) was developed to evaluate yield advantages to intercropping (Walker, 2009) and is preferable and has merit in that it can be applied to any intercropping situation (Willey, 1979). In this study it was consistently shown that, over both seasons, intercropping taro with bambara groundnut was more productive than growing either of the two crops in pure stands. The findings of this study concur with de la Peña and Melchor (1993) that intercropping taro with beans and other legumes was productive. Moreover, we showed that intercropping taro with bambara groundnut at a ratio of 1:1 was most productive and had no effect on corm yield of taro as the main crop, while also producing acceptable yields of bambara groundnut.

Results of this study suggest that taro and bambara groundnut are complimentary crops. Such complementarity may derive from benefits of leaf shading by taro – lowering air

temperatures to near optimum, lowering of soil evaporation as well as reduced incidence of weeds, pests and diseases (Midmore, 1993). Some of the benefits were visible during the trials, in terms of frequency of weeding – intercrop plots required less weeding compared with sole crop plots. This could represent savings in labour for the household, allowing for more time to be allocated to other tasks. In addition, bambara groundnut matured fast (on average 140 days after planting – data not shown) compared with an average of 210 days after planting in taro (data not shown) ensuring ease of harvest. The different maturity dates for bambara groundnut and taro would also ensure availability of food while the household waits to harvest taro – the main crop. Furthermore, this would result in an increase in the dietary nutrients produced by the farmers per unit area of land in a sustainable way.

## **5 Conclusion**

This study shows that intercropping taro with bambara groundnut at a ratio of 1:1 has no deleterious effect on growth of both taro and bambara groundnut. Growth of taro was mostly affected by rainfall distribution during the season; future research will focus on selection of planting dates as a management tool for managing rainfall distribution associated water stress. Inclusion of bambara groundnut (a nitrogen-fixing plant) in taro cropping systems is complimentary in that taro and bambara groundnut roots extract water from different depths of the soil profile while intermingling of roots improves utilization of soil nutrients. Intercropping taro with bambara groundnut is highly productive, in terms of additional output per unit area of land accrued from the bambara groundnut crop, with no significant negative effect on yield of the main crop - taro. The 1:1 intercrop had an LER of 1.53 compared to 1.23 for the 1:2 intercrop, indicating there was an advantage to intercropping. Lastly, intercropping taro with bambara groundnut is productive, sustainable and beneficial such that it improves farmers' nutritional productivity per unit area of land under cultivation compared with sole cropping taro.

## **Acknowledgements**

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## **References**

**(See final references list pages 198-228)**

## CHAPTER 8

### CALIBRATION AND VALIDATION OF AQUACROP MODEL FOR TARO (*COLOCASIA ESCULENTA* L. SCHOTT) AND BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA* L. VERDC) LANDRACES

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## SUMMARY

Promotion of neglected underutilised species as possible future crops under water-limited conditions hinges on availability of empirical information describing their yield responses to water. Therefore, AquaCrop was calibrated and validated for taro and bambara groundnut landraces from South Africa, using data from pot, field and rainshelter experiments conducted over two seasons (2010/11 and 2011/12) at two locations (Pretoria and Pietermaritzburg) representative of semi-arid climates. Observed weather and soil physical parameters for specific sites together with measured crop parameters for taro and bambara groundnut from optimum experiments conducted during 2010/11, were used to develop climate, soil and crop files in AquaCrop and to calibrate the model. The calibration for taro showed a good fit ( $R^2 = 0.789$ ; RMSE = 2.380%;  $d = 0.920$ ) for canopy cover (CC) as well as for final biomass (RMSE = 1.350 t ha<sup>-1</sup>) and yield (RMSE = 1.205 t ha<sup>-1</sup>). Calibration for bambara groundnut showed a very good fit for CC ( $R^2 = 0.940$ ; RMSE = 3.367%;  $d = 0.989$ ) and biomass ( $R^2 = 0.957$ ; RMSE = 1.290 t ha<sup>-1</sup>;  $d = 0.998$ ). The model also predicted final biomass (RMSE = 1.695 t ha<sup>-1</sup>) and yield (RMSE = 0.294 t ha<sup>-1</sup>) of bambara groundnut reasonably well. Validation of bambara groundnut showed good fit for CC under irrigated ( $R^2 = 0.858$ ; RMSE = 9.717%;  $d = 0.956$ ) and rainfed field conditions ( $R^2 = 0.951$ ; RMSE = 6.176%;  $d = 0.975$ ) compared with simulation of results from rainshelter experiments. The model also simulated final biomass and yield of bambara groundnut very well under field conditions. Regarding to taro, the model showed good simulation for CC under irrigated conditions ( $R^2 = 0.844$ ; RMSE = 1.852%;  $d = 0.998$ ), but it underestimated CC under rainfed ( $R^2 = 0.018$ ; RMSE = 20.170%;  $d = 0.645$ ) conditions. The model predicted biomass ( $R^2 = 0.898$ ; RMSE = 5.741 t ha<sup>-1</sup>;  $d = 0.875$ ) and yield ( $R^2 = 0.964$ ; RMSE = 1.425 t ha<sup>-1</sup>;  $d = 0.987$ ) reasonably well. The model also predicted taro biomass ( $R^2 = 0.996$ ; RMSE = 1.745 t ha<sup>-1</sup>;  $d = 0.985$ ) and yield ( $R^2 = 0.980$ ; RMSE = 1.266 t ha<sup>-1</sup>;  $d = 0.991$ ) well for the independent data set. Given that this was the first attempt to simulate biomass and yield for taro – an aroid – using AquaCrop, the model simulations were very satisfactory. Improvements to the model should consider the crop's distinctive growth pattern. The calibration and validation of AquaCrop for a local bambara groundnut landrace was successful.

## INTRODUCTION

Climate change forecasts have predicted increased occurrence and severity of droughts for South Africa (Hassan, 2006, de Wit and Stankiewicz, 2006), a situation that will increase the risk of crop failure. It is also perplexing that none of the current major crops are adapted for cultivation under water stressed conditions (Baye *et al.*, 2001); this poses a threat to food security in South Africa (Sisulu and Scaramella, 2012). Vulnerable communities have already been impacted by the slightest shift in weather; either the rains come a little bit early or they come a bit late, but by that time the community has lost their crop (Zabula, 2011). The unpredictability of future climate change coupled with the water scarcity situation has initiated interest in identifying underutilised indigenous and traditional crops as possible drought tolerant crops for the future in South Africa (Mabhaudhi, 2009). However, due to a possible bias in research in favour of major crops, scant information currently exists describing the agronomy and water use of such crops.

Taro (*Colocasia esculenta* L. Schott) and bambara groundnut (*Vigna subterranean* L. Verdc) fall within the category of underutilised indigenous and traditional crops in South Africa. Taro is a major root crop of the Araceae family with its centre of origin in the Indo-Malay regions (Kreike *et al.*, 2004; Lebot *et al.*, 2005). On the other hand, bambara groundnut, an indigenous African legume, originates between the Jos Plateau in Northern Nigeria and Garu in Cameroon (Pasquet *et al.*, 1999). Although both crops have their origins outside of South Africa, they have become “indigenised” over many years (>100 years) of cultivation and natural and farmer selection within South Africa (Schippers, 2002, 2006). Such selection, often occurring under harsh conditions, may have led to these crops “acquiring” drought tolerance. Moreover, landraces are thought to be resilient and possibly drought tolerant (Zeven, 1998).

Bambara groundnut is a protein rich crop (Ominawo *et al.*, 1999) cultivated throughout sub-Saharan Africa. Taro, on the other hand, is a starchy wetland crop associated with high levels of water-use. In South Africa, a great deal of taro production is rainfed and occurs inland under water limited conditions (Modi, 2004; Shange, 2004). Successful commercialisation of the crop (Modi, 2003) has led to increased taro production and expansion into areas with limited water availability. Lack of quantitative information



describing agronomy and water-use is a major hindrance to the promotion of both crops. With the threat of looming climate change and in the absence of extensive, and often costly, agronomic trials, the use of calibrated and validated crop models may prove useful to generate such information.

Crop models have proved to be useful tools for estimation of crop yields (Azam-Ali *et al.*, 2001; Steduto *et al.*, 2009; Singels *et al.*, 2010) and for comprehensive synthesis of quantitative understanding of physiological processes as well as for evaluating crop management options. However, crop models have not been fully explored for underutilised crops. There have been previous attempts to model bambara groundnut using several other models like the Predicting Arable Resource Capture in Hostile environment (PARCH – Bradley and Crout, 1993) model (Collinson *et al.*, 1996). This developed through to BAMnut (Bannayan, 2001; Azam-Ali *et al.*, 2001), subsequently to BAMFOOD (Cornelissen, 2005), ultimately leading up to BAMGRO (Karunaratne, 2009; Karunaratne *et al.*, 2010). Recently, Karunaratne *et al.* (2011) calibrated and validated AquaCrop for bambara groundnut.

AquaCrop (Raes *et al.*, 2009; Steduto *et al.*, 2009; Steduto *et al.*, 2012) is a water-driven FAO crop model suitable for simulating yield responses to water stress. The model has been previously used for several underutilised crops such as quinoa (Geerts *et al.*, 2009), bambara groundnut (Karunaratne *et al.*, 2011), orange fleshed sweet potato (Beletse *et al.*, 2011) and pearl millet (Bello *et al.*, 2011). The aim of this study was to calibrate and validate the FAO's AquaCrop model for taro and bambara groundnut landraces from South Africa.

## MATERIAL AND METHODS

### *Study site descriptions*

Field and rainshelter experiments (Table 1) were conducted at the Agricultural Research Council - Roodeplaat, Pretoria (25°60'S; 28°35'E; 1168 masl) and Ukulinga, Pietermaritzburg (29°37'S; 30°16'E; 775 masl), during the 2010/11 and 2011/12 summer seasons. Soil in field and rainshelter trials at Roodeplaat was classified as sandy loam and sandy clay loam, respectively (USDA taxonomic system) (Table 2). The average, within season rainfall

(November to April) of Roodeplaat is about 500 mm, and is highly variable with maximum precipitation in December and January. Daily maximum and minimum temperature averages are 34°C and 8°C in summer (November – April). Ukulinga represents a semi-arid environment and is characterised by clay-loam soils (USDA taxonomic system) (Table 2). The average, within season rainfall (November to April) of Ukulinga is 738 mm, with most of it being received in November, December and January.

Table 1. Summary of experiments used to develop model parameters for calibration and validation of AquaCrop.

<b>Experiment</b>	<b>Location</b>	<b>Crop</b>	<b>Treatment</b>	<b>Season</b>
<b>Calibration</b>				
Pot trials	CERU (KZN-PMB)	Taro and bambara groundnut	No stress, intermittent stress & terminal stress	2010
Field	Pretoria (ARC-VOPI)	Bambara groundnut	Irrigated & Rainfed	2010-11
Field	Ukulinga, (KZN-PMB)	Taro	Irrigated & Rainfed	2010-11
Rain shelter	Pretoria (ARC-VOPI)	Taro and bambara groundnut	100% Eta	2010-11
<b>Validation</b>				
Field	Ukulinga, (KZN-PMB)	Taro	Irrigated & Rainfed	2011-12
Rain shelter	Pretoria (ARC-VOPI)	Taro and bambara groundnut	30, 60 & 100% Eta	2011-12
*Field	Umbumbulu, KZN	Taro	Rainfed	2007-08

\*Experiments were described by Mare and Modi (2009).

Table 2. Soil descriptions and properties of each experimental site and the inputs entered in AquaCrop to develop the soil file.

<b>Location</b>	<b>Textural class</b>	<sup>v</sup> <b>PWP</b> ———— vol % ————	<sup>w</sup> <b>FC</b>	<sup>x</sup> <b>SAT</b>	<sup>y</sup> <b>TAW</b> (mm m <sup>-1</sup> )	<sup>z</sup> <b>Ksat</b> (mm day <sup>-1</sup> )
Ukulinga	Clay	28.3	40.6	48.1	123	25.0
Roodeplaat	Sandy loam	10.0	22.0	41.0	120	500.0
Rainshelter (Taro)	Sandy clay loam	16.1	24.1	42.1	80	324.2
Rainshelter (Bambara groundnut)	Sandy loam	12.6	19.9	42.8	73	663.6

<sup>v</sup>PWP – permanent wilting point; <sup>w</sup>FC – field capacity; <sup>x</sup>SAT – saturation; <sup>y</sup>TAW – total available water; <sup>z</sup>Ksat – saturated hydraulic conductivity.

### *Experiments*

Controlled (pot), field and rainshelter experiments were conducted for taro and bambara groundnut landraces in order to develop crop specific parameters and to calibrate and validate the FAO AquaCrop model.

*Plant materials.* Three taro landraces – Dumbe Lomfula, KwaNgwanase and Umbumbulu, were collected from different areas in KwaZulu-Natal, South Africa. Dumbe Lomfula is a wild type; KwaNgwanase is semi-domesticated while the Umbumbulu landraces is well-domesticated and widely cultivated inland. A bambara groundnut landrace was collected from Jozini, KwaZulu-Natal and characterised into three selections (Brown, Light-brown and Red) based on seed coat colour

*Pot trials.* The objective of the pot trials was to evaluate emergence, canopy expansion and stomatal closure and their sensitivity to water stress. These trials were conducted during 2010 under simulated drought conditions, for both taro and bambara groundnut, in tunnels at the University of KwaZulu-Natal, Pietermaritzburg. The experimental layout was a completely randomised design (CRD) with two factors: landrace type (3) and water stress (no stress,

intermittent stress and terminal stress), replicated six times. Details of experimental designs, procedures and measurements taken are described in Mabhaudhi *et al.* (2011, 2012).

*Rainshelters trials.* The objective of the rainshelter experiments was to evaluate growth, yield and water-use of taro and bambara groundnut landraces in response to a range of water regimes. With regards to modelling, the experiments were designed to contribute in developing parameters for maximum canopy cover and effect of stress on canopy expansion as well as stomatal conductance.

The experiments were conducted during 2010/11 and 2011/12 growing seasons at Roodeplaat, Pretoria. The experimental design was a factorial experiment laid out in a randomised complete block design with two factors: irrigation level and landrace type (3), replicated three times. The three irrigation levels were 30, 60 and 100% of crop water requirement (ETa), delivered using drip irrigation system. The rainshelters have a total area of 288 m<sup>2</sup>, with individual plot size of 6 m<sup>2</sup>. Plant spacing was 0.6 m x 0.6 m for taro and 0.3 m x 0.3 m for bambara groundnut. The rainshelters operate on electric power and automatically cover the experimental crop when it is raining, but otherwise remain open, positioned at least 5 m from the field. Therefore, except when it was raining, the crops experienced normal field conditions.

*Field trials.* The objective of these trials was to determine the mechanisms involved in taro and bambara groundnut landraces' drought tolerance under field conditions. Data collected from these experiments contributed in developing parameters for time to emergence, initial cover, times to maximum canopy cover, senescence and maturity as well as harvest index.

Taro was planted during 2010/11 and 2011/12 growing seasons at Ukulinga, Pietermaritzburg, in a split-plot design arranged in a randomised complete block design. Irrigation [full irrigation (FI) versus rainfed (RF)] was the main factor with landrace type (3) as sub-factors, replicated three times. The total size of the field trial was 499.8 m<sup>2</sup>. Main plots (FI and RF) measured 207.4 m<sup>2</sup> each, with 15 m spacing between them and sprinklers were designed to have a maximum range of 6 m radius to prevent water sprays from reaching RF plots. Sub-plot size was 17 m<sup>2</sup> with an inter-plot spacing of 1 m, and plant spacing of 1 m x 0.5 m, translating to 20 000 plants per hectare. Irrigation scheduling for the FI treatment was

based on  $ET_0$  and a crop factor. During the 2010/11 growing season, 912 mm of rainfall were compared to 622 mm received during 2011/12 growing season. Supplementary irrigation amounted to 879 mm and 740 mm during 2010/11 and 2011/12 growing seasons, respectively. Less supplementary irrigation was applied during 2011/12 growing season because the taro crop was harvested earlier than in the preceding season.

Bambara groundnut field trials were planted at Roodeplaat, on an area of 144 m<sup>2</sup>. Main plots were 52 m<sup>2</sup> each with spacing of 10 m between them, and sub-plots measuring 3 m<sup>2</sup>. Plant spacing was 0.3 m x 0.2 m. Field trials were irrigated using sprinkler irrigation scheduled using a crop factor and  $ET_0$ . The total amount of rainfall received during the experiments was 678 mm in 2010/11 and 466 mm during 2011/12 growing season. The 2010/11 growing season was characterised by less than average rainfall and was therefore a dry season. Supplementary irrigation supplied to the full irrigation treatment amounted to 526 mm during 2010/11 and 890 mm during 2011/12. The higher amount of supplementary irrigation applied during 2011/12 was because this was a drier season compared to 2010/11.

### *Agronomic practices*

For all trials, management was similar and kept at optimum during 2010/11 and 2011/12. Land preparation was done according to best agronomic practices. Fertiliser application was based on results of soil fertility analysis and applied using an organic fertiliser Gromor Accelerator (30 g N kg<sup>-1</sup>, 15 g P kg<sup>-1</sup> and 15 g K kg<sup>-1</sup>). Weekly observations of pests and diseases were done to ensure effective control. Routine weeding and ridging were done to prevent weeds from competing with crops for water, nutrients and radiation.

### *Measurements*

Experimental designs and data collection were specifically designed to collect empirical data that would be used for modelling both taro and bambara groundnut landraces. Soil physical characteristics (soil depth, soil texture, bulk density and gravimetric field capacity) were determined for each experimental site (field trials and rainshelters). The Soil Water

Characteristics                      Hydraulic                      Properties                      Calculator  
(<http://hydrolab.arsusda.gov/soilwater/Index.htm>) was then used to calculate volumetric soil water content at field capacity (FC), permanent wilting point (PWP), saturation (SAT) and saturated hydraulic conductivity (Ksat) (Table 2). These were also used to develop the soil files for the respective sites in AquaCrop.

Daily weather parameters (maximum and minimum air temperature, relative humidity, solar radiation, wind speed, rainfall and ET<sub>o</sub>) for the duration of the experiments were recorded and collected from automatic weather stations located within 100 m radii from each of the field and rainshelter experiments. These were used to create climate files for each experiment in AquaCrop for the respective sites. The climate file for the rainshelter experiments excluded rainfall.

Soil water content (SWC) in pot trials was monitored gravimetrically by periodic weighing of pots and electronically using an ML-2x Theta probe. In the rainshelters, SWC was monitored using ML-2x Theta Probes connected to a DL-2 data logger (Delta-T Devices, UK). In each plot, two probes were carefully inserted within the root zone at depths of 30 cm and 60 cm, respectively, and then buried with soil. The frequency of data collection for SWC using the Theta probes was every 4 hours. In the field trials, SWC was measured using gravimetric sampling and a PR2/6 profile probe connected to an HH-2 moisture meter (Delta-T Devices, UK) at depths of 10, 20, 30, 40, 60 and 100 cm.

*Pot trials.* Daily emergence was counted; up to 35 and 49 days after planting (DAP) for taro and bambara groundnut landraces, respectively. Weekly data were collected to determine leaf number, plant height, leaf area (Modi, 2007) and stomatal conductance. Measurements of seedling leaf area for taro's Umbumbulu landrace and the 'Red' bambara groundnut landrace selection were also used to develop the parameter for seedling leaf area in AquaCrop.

*Field and rainshelter experiments.* Time to emergence (DAP) was defined as the time taken to achieve 90% emergence as stated in AquaCrop (Raes *et al.*, 2009) and was counted weekly for taro and bambara groundnut, respectively. Destructive sampling was done at full emergence to determine seedling leaf area (cm<sup>2</sup>), root length and biomass. Measured seedling leaf area for taro's Umbumbulu landrace and the 'Red' bambara groundnut landrace selection were used to

complement pot trial data and used to describe seedling leaf area in AquaCrop. Measurements of seedling root length taken at full emergence were used to determine the parameter for minimum rooting depth ( $Z_{r_{min}}$ ). Stomatal conductance was measured using a steady state leaf porometer (Model SC-1, Decagon Devices, USA) and used to describe crop sensitivity (stomata) to water stress in AquaCrop.

Leaf area index (LAI) index was measured using the LAI 2200 Canopy Analyser (Li-Cor, USA & Canada). However, measurements of LAI were not used to calculate canopy cover (CC) for AquaCrop. Instead, diffuse non-interceptance (DIFN), which is an output of the LAI 2200 canopy analyser, was used to determine CC. In essence, DIFN is calculated by integrating the gap fraction (GAPS) to obtain a value indicative of the fraction of the sky that is NOT obscured by the plant's canopy. The value of DIFN ranges from 0 (no sky visible to the sensor) to 1 (no canopy obscuring the sun) (LAI 2200 Manual, 2010). Thus, it may be argued that DIFN is more indicative of actual canopy cover than LAI; thence there is no need to convert LAI to CC (Abraham Singels, pers. comm., 2011). Therefore CC was obtained from DIFN as follows;

$$1 - DIFN = CC \quad \text{Equation 1}$$

Canopy cover values observed in field and rainshelter trials for taro's Umbumbulu landrace and the 'Red' bambara landrace selection were used to develop parameters for maximum canopy cover ( $CC_x$ ) and time taken to achieve  $CC_x$  which were entered in AquaCrop. Observations of canopy cover under irrigated and rainfed conditions as well as using the 60% and 30% ETa treatments from rainshelter experiments were used to describe crop sensitivity to water stress in AquaCrop.

Measurements of biomass were routinely collected for evaluation of crop water productivity, development and dry matter partitioning. Final biomass, yield and harvest index (HI) were determined at harvest. The occurrence of major phenological stages, timing and duration of flowering, times to senescence and maturity, was recorded in days after planting (DAP). A phenological stage was deemed to have either occurred or been completed if and when it was observed in at least 50% of experimental plants. Data were later converted to thermal time according to the Method 2 as described by McMaster and Wilhelm (1997);

$$GDD = \left[ \frac{(T_{max} + T_{min})}{2} \right] - T_{base} \quad \text{Equation 2}$$

where GDD = growing degree days

$T_{max}$  and  $T_{min}$  = maximum and minimum temperature, respectively, and

$T_{base}$  = base temperature for the crop

Where if  $T_{max} < T_{base}$ , then  $T_{max} = T_{base}$  and if  $T_{min} < T_{base}$ , then  $T_{min} = T_{base}$

Thereafter, simulations for taro's Umbumbulu landrace and the 'Red' bambara groundnut landrace selection were performed in AquaCrop as described by Steduto *et al.* (2009) and Raes *et al.* (2009). Table 1 gives a detailed list of the experiments used to calibrate and validate AquaCrop for taro's Umbumbulu landrace and the 'Red' bambara groundnut landrace selection. For taro, independent results from experiments conducted by Mare and Modi (2009) were also used to test the model's accuracy under dryland conditions. Validation for Mare and Modi (2009) was for the *Dumbe dumbe* landrace which is the vernacular name for the Umbumbulu landrace used to calibrate taro in this study.

### *Model evaluation*

Goodness of fit of AquaCrop outputs against observed field measurements was evaluated using the coefficient of determination ( $R^2$ ), root mean square error and its components (RMSE, RMSEs and RMSEu) and Willmott's coefficient of agreement (*d-index*). The coefficient of determination ( $R^2$ ) is used for comparison of observed (O) and predicted (P) values. It shows goodness of fit between observed and predicted values. It is however, dependent on the number ( $n$ ) of data sets used.

Willmott (1981) proposed the use of RMSE and its systematic (RMSEs) (biased or non-random) and unsystematic (RMSEu) (unbiased or random) components as alternative measures of model performance. For interpretation of results, RMSEs should approach zero, while the RMSEu should approach RMSE in order for a model's performance to be deemed as



“good”. The systematic (RMSEs) and unsystematic (RMSEu) components are computed as follows;

$$RMSE_s = \left[ n^{-1} \sum_{i=1}^n (\hat{P}_i - O_i)^2 \right]^{0.5} \quad \text{Equation 3}$$

$$RMSE_u = \left[ n^{-1} \sum_{i=1}^n (P_i - \hat{P}_i)^2 \right]^{0.5} \quad \text{Equation 4}$$

$$RMSE = (RMSE_s + RMSE_u)^{0.5} \quad \text{Equation 5}$$

where,  $n$  = the number of observations, and  $\hat{P}_i$  is derived from  $\hat{P}_i = a + b.O_i$  whereby  $a$  and  $b$  are the intercept and slope, respectively, of a least regression between the predicted (dependent variable) and observed (independent variable) values.

In addition to computing RMSE and its systematic (RMSEs) and unsystematic components (RMSEu), Willmott (1981) further suggested an index of agreement ( $d$ ) which reflects the degree to which the observed values are accurately estimated by the model. This is computed as follows;

$$d = 1 - \frac{\sum_{i=1}^n (P_i - O_i)^2}{\sum_{i=1}^n \left[ |P'_i| + |O'_i| \right]^2}, \quad 0 \leq d \leq 1 \quad \text{Equation 6}$$

where,  $P'_i = P_i - \bar{O}$  and  $O'_i = O_i - \bar{O}$  whereby  $\bar{O}$  is the observed means.

Willmott's index of agreement ( $d$ ) is a measure of the degree to which a model's predictions (P) are error free or the degree to which observed deviations about observed means

( $\bar{O}$ ) correspond, both in size and sign, to predicted deviations about  $\bar{O}$ . Concurrently, the *d-index* is a standardised measure developed with the intention that (i) it may be easily interpreted, and (ii) cross-comparisons of its magnitudes for a variety of models, regardless of units, could be readily made. The *d-index* varies between 0.0 – indicating complete disagreement, and 1.0 – indicating complete agreement between observed and predicted values. According to Wilmott (1981), the *d-index* often complements information contained in RMSE, RMSEs and RMSEu. Therefore, in addition to the use  $R^2$ , evaluation of crop models should also include RMSE, RMSEs, RMSEu and the *d-index*.

### AQUACROP MODEL DESCRIPTION

AquaCrop is a water-driven, canopy level, engineering type model (Steduto *et al.*, 2009; Raes *et al.*, 2009; Steduto *et al.*, 2012). It pays particular emphasis to simulating yield response to water under both irrigated and rainfed conditions. The model was born out of previous efforts by Doorenbos and Kassam (1979) in FAO’s Irrigation and Drainage Paper No. 33. The calculation steps and procedures of AquaCrop have been described by Steduto *et al.* (2009) and Raes *et al.* (2009). At the core of the model is the following equation:

$$\mathbf{B} = \mathbf{WP} \times \Sigma \mathbf{Tr} \quad \text{Equation 7}$$

where,  $\mathbf{B}$  = biomass,

$\mathbf{WP}$  = water productivity (biomass per unit of cumulative transpiration), and

$\mathbf{Tr}$  = crop transpiration

Underlying Eq. 7 is AquaCrop’s development which allows it to (1) separate ET into  $\mathbf{Tr}$  and soil evaporation ( $\mathbf{E}$ ), (2) use the latter as inputs in a simple canopy growth model, (3) describe final yield ( $\mathbf{Y}$ ) as a function of  $\mathbf{B}$  and harvest index ( $\mathbf{HI}$ ), and (4) segregate effects of water stress into four primary components; canopy growth, canopy senescence, crop transpiration and  $\mathbf{HI}$ . Each of these stress response factors, excluding  $\mathbf{HI}$ , has its own stress coefficient  $\mathbf{K}_s$ , which acts as an indicator of the stress’ intensity. In practise,  $\mathbf{K}_s$  is a modifier or correction factor for its target model parameter. Its value varies from 0 - 1, with zero

representing maximum possible effect of the stress and one indication no stress (Steduto *et al.*, 2009).

At the heart of Eq. 7 is WP which has been described by Hanks (1983) and Tanner and Sinclair (1983) as a parameter that remains constant across different soils and climatic conditions. When WP is normalised for different climatic conditions using CO<sub>2</sub>, this further makes it a conservative parameter (Steduto *et al.*, 2007). This implies the applicability, robustness as well as transferability of model calibrations among users all over the world.

Figure 1 illustrates the functional relationships between the different components of AquaCrop. As with other models, AquaCrop includes the soil (soil water balance), the plant and the atmosphere as structural components of the model (Steduto *et al.*, 2009). The atmosphere and soil components bear similarities to other models. It is the relationship between the plant and soil components that distinguishes AquaCrop from other known models – that is discussed here.

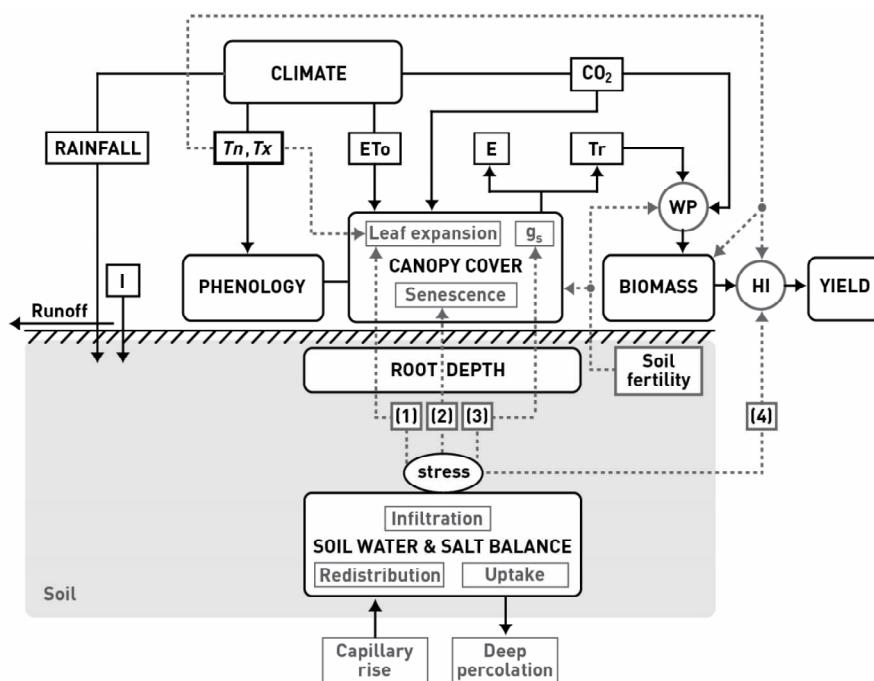


Figure 1. Flowchart of AquaCrop indicating the structural relationships in the SPAC (adapted from Raes *et al.*, 2009).

AquaCrop models the crop based on five major components and their associated responses to water stress. These are, phenology/development, canopy cover, rooting depth, biomass production and harvestable yield (Raes *et al.*, 2009). The crop responds to water stress by (1) limiting canopy expansion, (2) early canopy senescence, and (3) closure of stomata (Raes *et al.*, 2009). Under continued water stress, the (4) WP and (5) HI parameters may also be affected. It is important to note that three of these responses occur at the canopy level, hence the importance of the canopy in AquaCrop. Collectively, these five responses form the background framework of the crop component of AquaCrop (Steduto *et al.*, 2009).

In AquaCrop, the canopy, through green canopy cover and canopy duration, represents the source of Tr. It is Tr that gets translated to biomass (B) through WP (Eq. 7). Following this, yield (Y), which is a constituent of B is then determined as a function of HI;

$$\mathbf{Y = B*HI} \qquad \mathbf{Equation 8}$$

The canopy, through its expansion, ageing, conductance and senescence, is very important in AquaCrop. The canopy is directly linked to Tr, which is directly related to B through Eq. 7, and indirectly to Y through Eq. 8. Under non-limiting conditions, canopy growth is exponential during the period from emergence to maximum canopy cover (CC<sub>x</sub>). Canopy cover duration is also a function of time and is dependent on the determinacy of the crop, aspects all of which can be varied by the user in AquaCrop. Beyond this point, the canopy follows an exponential decay (Raes *et al.*, 2009).

Unlike all other models, AquaCrop uses canopy cover (CC) not leaf area index (LAI) – a distinctive feature of AquaCrop. The use of CC, as opposed to LAI, is meant to introduce simplicity by reducing overall above-ground growth into just a single growth function. The crop's rooting system is also considered in AquaCrop through crop parameters for effective rooting depth (Z) and the crop's water extraction pattern. The effective rooting depth is defined as the depth at which the crop will conduct most of its water uptake (Raes *et al.*, 2009).

Temperature x varietal differences are also catered for in AquaCrop. The model provides the user with two simulation modes – thermal time (GDD) and calendar time. The model itself uses thermal time (Raes *et al.*, 2009) based on Method 2 as described by McMaster and

Wilhelm (1997). There is an important modification in AquaCrop in that there is no adjustment for  $T_n$  when and if it falls below base temperature ( $T_b$ ). This allows for better and more realistic considerations of temperature fluctuations below  $T_b$  and allows for effective simulation of winter crops (Steduto *et al.*, 2009; for algorithms see Raes *et al.*, 2009).

## CALIBRATION

Crop parameters used to calibrate AquaCrop for taro's Umbumbulu landrace and the 'Red' bambara groundnut landrace selection were derived from controlled, field and rainshelter experiments representing a wide range of water regimes and environmental conditions and soils (Tables 1 and 2). Selection of landraces was based on results from pot, field and rainshelter experiments which showed 'Umbumbulu' and the 'Red' landrace selection as the most stable, in terms of within landrace variability, and adapted (to water-limited conditions) landraces of taro and bambara groundnut, respectively.

Initial calibration involved matching observed CC to simulated CC. Subsequent to this; the model was calibrated by comparing observed and simulated biomass (B) and yield (Y). Calibration included adjusting selected parameters within a known range of fluctuation to represent within landrace variation. Data used for calibration were not used for validation. The reduced input requirements of the model, compared to others, enhanced the ease of calibration. Crop parameters used to calibrate taro and bambara groundnut landraces are summarised in Tables 3 and 5.

Table 3. Preliminary input parameters for the ‘Red’ bambara groundnut landrace selection in AquaCrop

<b>Parameter</b>	<b>Description</b>	<b>Model Input</b>
T <sub>base</sub>	Base temperature (°C)	9*
T <sub>upper</sub>	Cut-off temperature (°C)	30*
Emergence	Time to 90% emergence	299
CC <sub>x</sub>	Maximum canopy cover (%)	85
Time to CC <sub>x</sub> (GDD)		1155
Zr <sub>max</sub>	Maximum rooting depth (m)	1.0
Zr <sub>min</sub>	Minimum rooting depth (m)	0.10
Canopy senescence	Time to canopy senescence	1814
Start of yield formation		1047
Duration of flowering		629
Length of HI build up		1024
Maturity		2227
Soil water depletion factor canopy expansion (p-leaf) Upper Limit		0.50*
Soil water depletion factor canopy expansion (p-leaf) Lower Limit		0.80*
Shape factor for water stress coefficient leaf expansion		1.00*
Soil water depletion for stomatal control (p-stomatal)		0.80*
Shape factor for water stress coefficient stomatal control		2.00*
Soil water depletion for canopy senescence (p-senescence)		0.90*
Shape factor for water stress canopy senescence		3.00*
Root expansion rate (cm/day)		1.2
Shape factor for root expansion		2.00*
Canopy cover per seedling (cm <sup>2</sup> )		2.00
Canopy growth coefficient p(CGC): increase in CC/ degree day		0.942
Canopy declining coefficient (CDC) per degree day		0.600
K <sub>cb</sub>		1.15
Normalised water productivity (WP) g m <sup>-2</sup>		11 <sup>x</sup>
Harvest index (percentage)		20 <sup>y</sup>
Positive effect of HI as result of limited growth in vegetative period		Moderate
Positive effect of HI as result of water stress affecting leaf expansion		Moderate
Water stress during flowering (p-upper)		0.90*
Negative effect on HI as a result of water stress inducing stomatal closure		Strong
Aeration stress		Sensitive

\*Parameters described by Karunaratne *et al.* (2011); <sup>x</sup>WP differed for the rainshelter experiments and was set at 10; <sup>y</sup>HI for the rainshelter experiments was 15%.

### *Calibrating bambara groundnut*

Since AquaCrop was previously calibrated for bambara groundnut by Karunaratne *et al.* (2011), calibration started with fine-tuning their crop file to South African local conditions. Time to emergence was observed in pot, field and rainshelters as days after planting (DAP) as 35 DAP and converted to GDD in AquaCrop (Table 3).

In order to determine  $CC_o$ , destructive sampling was done when the crop had achieved 90% emergence in all trials (field, rainshelter, pot and seedling establishment trials). Measured values of seedling leaf area observed were entered in AquaCrop as  $2.0 \text{ cm}^2$  (Table 3) compared to  $5.0 \text{ cm}^2$  described by Karunaratne *et al.* (2011). This was acceptable since our experimental conditions and landraces were different to those used by Karunaratne *et al.* (2011). Thereafter, the model used initial seedling leaf area to compute  $CC_o$ . Observed values for maximum canopy cover ( $CC_x$ ), times taken to achieve  $CC_x$  and leaf senescence were input in AquaCrop (Table 3). Thereafter, using these observed values, the model computed canopy growth and decline coefficients (CGC and CDC) (Table 3).

Minimum rooting depth ( $Zr_{\min}$ ) was entered in AquaCrop as 0.10 m. (Table 3). Destructive sampling in field and rainshelter trials showed maximum root length of about 0.30 m; however, for better simulation a value of 1.0 m described by Karunaratne *et al.* (2011) was entered in AquaCrop as  $Zr_{\max}$  (Table 3). The time taken to achieve maximum rooting depth was also entered in AquaCrop. Based on these observed parameters, the model then derived root expansion rate as described in Raes *et al.* (2009).

Karunaratne *et al.* (2011) reported that AquaCrop's default settings for describing a grain crop were reasonably good for simulating bambara groundnut under both irrigated and rainfed conditions – our own calibration concurred with their assertion. A WP value of 11 was used and harvest index was calculated as 20% and entered in AquaCrop. This provided good simulation for final biomass and yield.

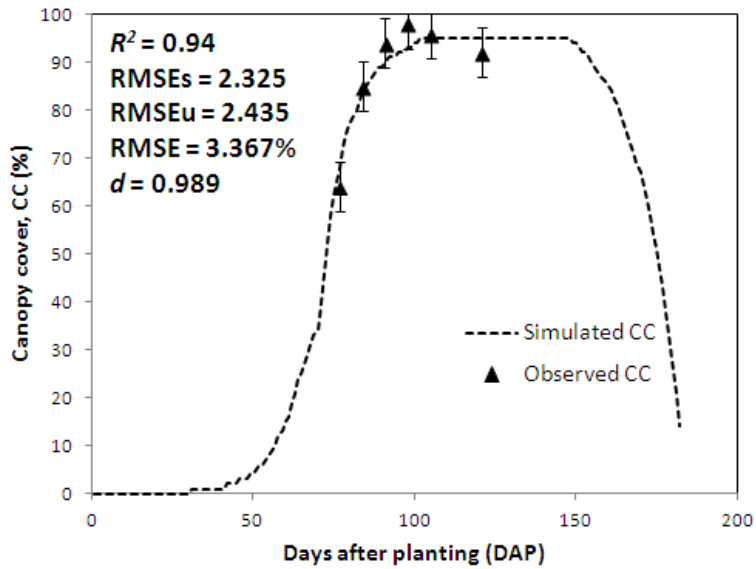


Figure 2. Calibration results of bambara groundnut canopy cover (CC %) under irrigated conditions (field trials) during 2010/11 growing season at Roodeplaat, Pretoria. Vertical bars indicate +/- standard error of means.

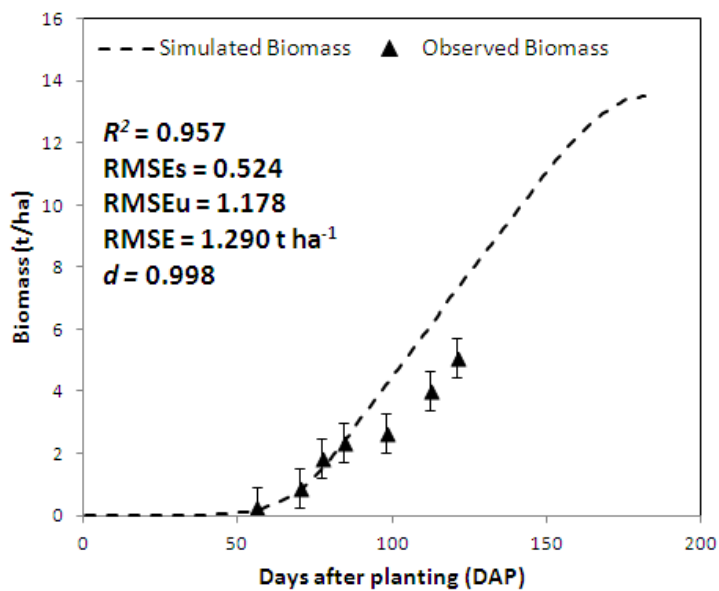


Figure 3. Calibration results of bambara groundnut biomass accumulation (t ha<sup>-1</sup>) under irrigated conditions (field trials) during 2010/11 growing season at Roodeplaat, Pretoria. Vertical bars indicate +/- standard error of means.



Results for calibration showed a reasonably good goodness of fit for both canopy cover and biomass (Fig 2 and 3). The coefficient of determination ( $R^2$ ) for CC was 0.94 and for biomass  $R^2$  was 0.957. Therefore, the model was able to predict CC and biomass reasonably well. The RMSE for CC was 3.37% which was very good compared to a RMSE of 14.79% reported by Karunaratne *et al.* (2011) for their calibration of four bambara groundnut landraces. They concluded that RMSE of 14.79% was very acceptable given the huge amount of variation that exists between and within bambara groundnut landraces. They further stated that high RMSE observed for biomass was due to a carry-over effect from the error from CC.

Results of final biomass and yield showed good comparison between predicted and observed biomass and yield (Table 4). The model over-estimated final biomass by 14% and yield by about 8.79% compared to observed biomass and yield; this may be regarded as acceptable. The margin of error for predicted biomass and yield is still within acceptable margins and may be due to the carry-over error from simulation of CC and cumulative B.

Table 4. Calibration results of final biomass and yield (simulated vs. observed) for irrigated (FI) field trials of taro's Umbumbulu landrace and 'Red' bambara groundnut landrace selection conducted during 2010/11.

	<b>Bambara groundnut</b>		<b>Taro</b>	
	<b>Biomass (t ha<sup>-1</sup>)</b>	<b>Yield (t ha<sup>-1</sup>)</b>	<b>Biomass (t ha<sup>-1</sup>)</b>	<b>Yield (t ha<sup>-1</sup>)</b>
<b>Observed</b>	11.80	3.341	20.7	17.1
<b>Simulated</b>	13.495	3.635	22.05	18.305
<b>RMSE</b>	1.695	0.294	1.350	1.205

### *Calibrating taro*

Taro was calibrated in AquaCrop using measurements from the optimum irrigated (FI) field trials conducted at Ukulinga during 2010/11. The optimum treatment (100% ETa) from the rainshelter trials conducted at Roodeplaar during 2010/11 was also used to develop as well as to confirm some parameters (Table 5). Rainfed trials were also used to fine-tune the calibrations.

Time to emergence for taro's Umbumbulu landrace was observed as 49 DAP; this was converted to GDD and entered in AquaCrop (Table 5). Observed seedling leaf area ( $25 \text{ cm}^2$ ) (Mabhaudhi *et al.*, 2012) was used to define seedling cover in AquaCrop. Together with plant density, AquaCrop then computed initial canopy cover ( $CC_o$ ) (Table 5). Observed  $CC_x$  and time taken to achieve  $CC_x$  were input in AquaCrop (Table 5). Using these, the model then derived the CGC (Table 5).

Observed times to senescence and maturity were input in AquaCrop; canopy decline coefficient (CDC) was then derived from these. However, contrary to observations of taro growth, the model derived value for CDC simulated canopy cover to reach zero about a month before harvest. Under actual conditions, unless frost occurs and kills off the foliage, taro's canopy can continue through winter as a perennial crop. Therefore, CDC was adjusted accordingly in order to obtain a better simulation of canopy decline (Table 5).

AquaCrop describes effects of water stress based canopy growth and senescence, crop transpiration and HI. Each of these stress response factors, excluding HI, has its own stress coefficient  $K_s$ , which acts as an indicator of the stress' intensity. Canopy growth, senescence and stomatal closure for taro's Umbumbulu landrace were entered in AquaCrop as sensitive to water stress. This was because results from field and rainshelter trials had shown that this landrace avoided drought by stomatal regulation (closure) and having a small canopy size. Thereafter, AquaCrop calculated p-values (Table 5) corresponding to these descriptions (Raes *et al.*, 2009). Since taro is naturally a wetland crop (Lebot, 2009), the crop was described in AquaCrop as tolerant to water logging (Table 5).

Table 5. Preliminary input parameters for taro's Umbumbulu landrace in AquaCrop

<b>Parameter</b>	<b>Description</b>	<b>Model input</b>
$T_{base}$	Base temperature (°C)	10
$T_{upper}$	Cut-off temperature (°C)	35
Emergence	Time to 90% emergence	460
$CC_x$	Maximum canopy cover (%)	85
Time to $CC_x$ (GDD)		1557
$Zr_{max}$	Maximum rooting depth (m)	0.8
$Zr_{min}$	Minimum rooting depth (m)	0.1
Canopy senescence	Time to canopy senescence	2115
Start of yield formation		1512
Length of build-up of HI		861
Maturity		2406
Soil water depletion factor canopy expansion (p-leaf) Upper Limit		0.10
Soil water depletion factor canopy expansion (p-leaf) Lower Limit		0.45
Shape factor for water stress coefficient leaf expansion		3.0
Soil water depletion for stomatal control (p-stomatal)		0.45
Shape factor for water stress coefficient stomatal control		3.0
Soil water depletion for canopy senescence (p-senescence)		0.45
Shape factor for water stress canopy senescence		3.0
Root expansion rate (cm/day)		0.6
Shape factor for root expansion		1.5
Canopy cover per seedling (cm <sup>2</sup> )		25
Canopy growth coefficient p(CGC): increase in CC/ degree day		0.698
Canopy declining coefficient (CDC) per degree day		0.577
$K_{cb}$		1.10
Normalised water productivity (WP) g m <sup>-2</sup>		15 <sup>x</sup>
Harvest index (percentage)		80 <sup>y</sup>
Positive effect of HI as result of limited growth in vegetative period		Moderate
Positive effect of HI as result of water stress affecting leaf expansion		Small
Negative effect on HI as a result of water stress inducing stomatal closure		Very strong
Aeration stress		Not stressed

<sup>x</sup>WP differed for the rainshelter experiments and was set at 22; <sup>y</sup>HI for the rainshelter experiments was 70%.

Our observations showed  $Z_{r_{max}}$  to range between 0.30 – 0.45 m. However, AquaCrop was unable to simulate for rainfed conditions using this value. This may be a result of our sampling procedure used to determine root depth as well as other soil factors. As such, following a series of simulations, a value of 0.8 m was used in AquaCrop for  $Z_{r_{max}}$  (Table 5) since it gave good results under both irrigated and rainfed conditions. This value corresponded to the model's description of a shallow-medium rooted crop; this concurs with the description of taro rooting depth suggested by Lebot (2009).

The model was able to simulate canopy cover (CC) (Fig 4) reasonably well ( $R^2 = 0.789$ ). Willmott's coefficient of agreement (*d-index*) showed very good agreement ( $d = 0.9196$ ) between predicted and observed CC for taro under irrigated (FI) conditions. Simulated final biomass (B) and yield (Y) also showed a very good fit with the observed data (RMSE = 1.350 and 1.205 t ha<sup>-1</sup>) (Table 4). Simulated B and Y were respectively, 6 and 7% greater than observed B and Y. This can be considered to be very good given that the model was simulating a landrace.

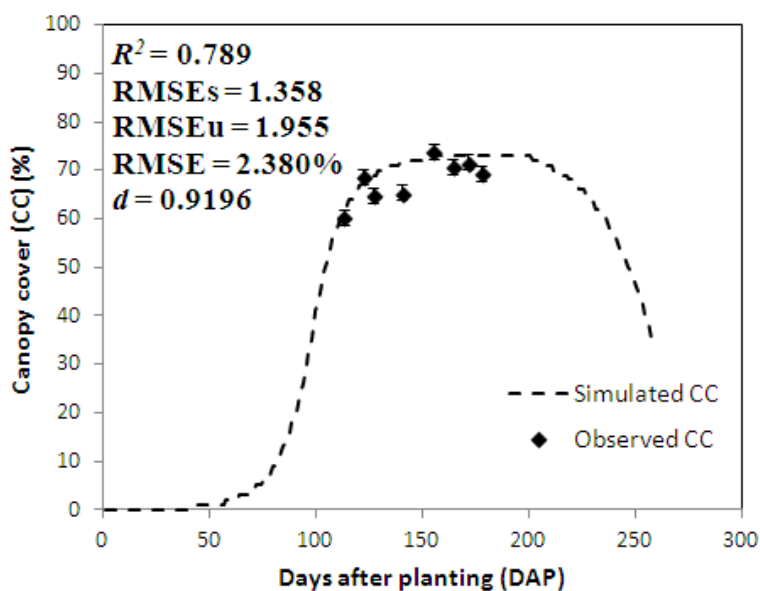


Figure 4. Calibration results of taro canopy cover (CC %) under irrigated conditions (field trials) during 2010/11 growing season at Ukulinga, Pietermaritzburg. Vertical bars indicate +/- standard error of means.

## VALIDATION

Subsequent to AquaCrop's calibration using data from optimum experiments conducted during 2010/11 season with no fertility or temperature stress, the model was validated for both bambara groundnut and taro using observed measurements from experiments [field (RF and FI) and rainshelter (100, 60 and 30% ETa)] conducted during 2011/12. In the case of taro, AquaCrop was also tested against independent data from previous experiments conducted by Mare and Modi, 2009 (Table 1).

### *Validating bambara groundnut*

Results of validation for the field trials showed a good fit between simulated and observed CC under irrigated ( $R^2 = 0.858$ ) (Fig 5A) and rainfed conditions ( $R^2 = 0.951$ ) (Fig 5B). Results also showed good agreement (*d-index*) between observed and simulated CC for irrigated ( $d = 0.9558$ ) (Fig 5A) and rainfed ( $d = 0.9746$ ) conditions (Fig 5B). The RMSE obtained from statistical analysis of simulated and observed values for rainfed and irrigated conditions was relatively low and similar to that obtained during calibration; this indicated model consistency and robustness. In addition, RMSEs was relatively low and close to zero, while RMSEu was shown to approach RMSE, thus indicating good model performance (Fig 5A and B). Therefore, the model showed very good simulation for rainfed production. This concurs with statements by Raes *et al.* (2009) and Steduto *et al.* (2009) that the model was especially useful for predicting yield under water-limited conditions.

Validation of the model using measurements from rainshelter experiments showed relatively good fit between observed and simulated CC under varying water regimes. Simulation of CC under optimum conditions (100% ETa) showed the best fit ( $R^2 = 0.951$ ) (Fig 6A) relative to 60% ( $R^2 = 0.901$ ) (Fig 6B) and 30% ETa ( $R^2 = 0.813$ ) (Fig 6C). The model managed to simulate well actual experimental observations that showed little difference in CC between the 100% and 60% ETa treatments (Fig 6A and B). In all three cases, the model was shown to under-estimate CC in the early and later parts of the season. This was also evidenced by the relatively lower agreement at 60% ( $d = 0.951$ ) (Fig 6 B) and 30% ( $d = 0.950$ ) (Fig 6C) compared with the 100% ETa treatment ( $d = 0.972$ ) (Fig 6A). This may account for the

relatively high RMSE obtained from statistical evaluation of model outputs (Fig 6A, B and C). The RMSE for CC simulated for the 100% ETa treatment was 14.055% (Fig 6A), which was similar to that reported by Karunaratne *et al.* (2011) for their calibration and validation of bambara groundnut. The RMSE, as well as its components (RMSEs and RMSEu), were shown to increase for the 60% and 30% ETa treatments (Fig 6B and C).

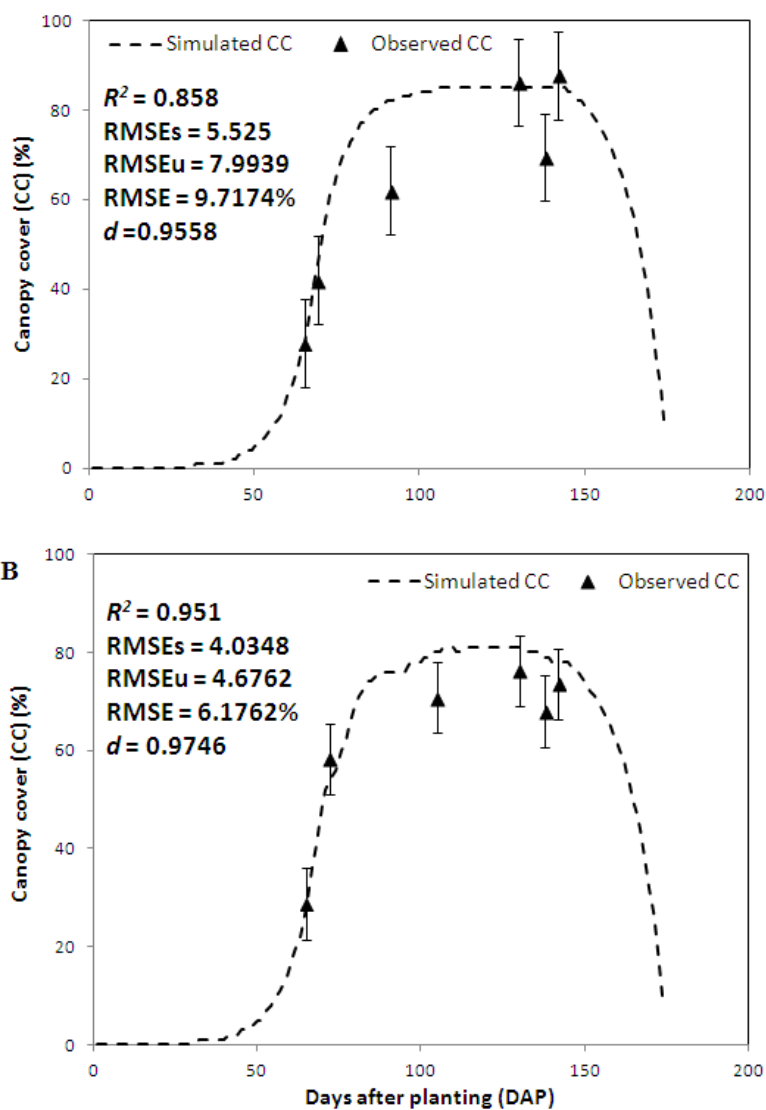


Figure 5. Validation of canopy cover (CC %) for bambara groundnut grown under A. Irrigated and B. Rainfed field conditions during 2011/12 growing season at Roodeplaat, Pretoria. Vertical bars indicate +/- standard error of means.

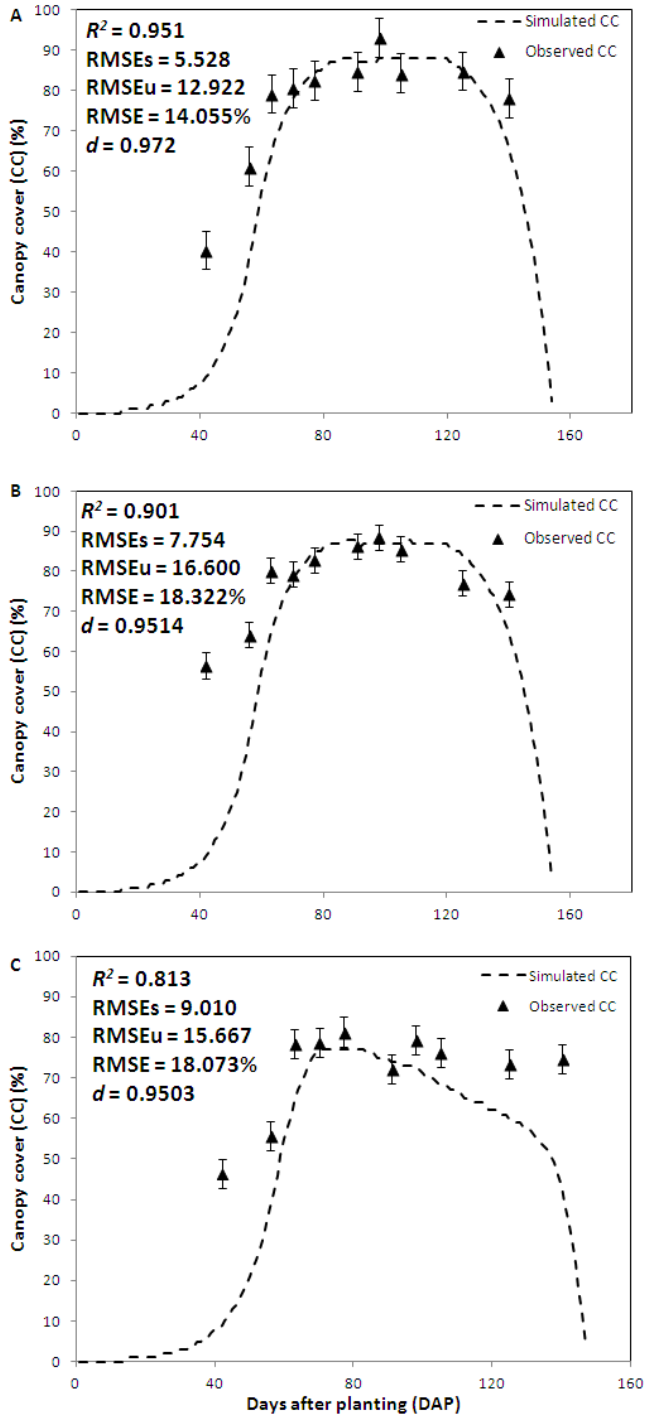


Figure 6. Validation of canopy cover (CC %) for bambara groundnut grown under A. 100% ETa, B. 60% ETa and C. 30% ETa in rainshelters during 2011/12 growing season at Roodeplaat, Pretoria. Vertical bars indicate +/- standard error of means.

The model predicted final biomass and yield very well for bambara groundnut grown under irrigated (FI) and rainfed (RF) field conditions (Table 6). The margin for error (RMSE) under field conditions (RF and FI) was relatively low, showing good model performance. However, the model did not show good prediction for biomass and yield for the three rainshelter irrigation treatments (100, 60 and 30% ETa) (Table 6). While Karunaratne *et al.* (2011) reported under-estimation of some landraces, in this study; the model was shown to over-estimate both biomass and yield in the rainshelter irrigation treatments (Table 6). The over-estimation of biomass and yield in the rainshelter may be due to carry-over error from simulation of CC. It is possible that model performance in the rainshelter may have been affected by periodic closing and opening of the shelter during rainfall events – this could have altered the microclimate in the rainshelter – a phenomenon which the model could not account for.

Over-all, despite the model’s performance with regards to the rainshelter irrigation treatments, the model was shown to predict well biomass under yield under field conditions (RF and FI). This further strengthens the model’s suitability for simulating yield response to water availability.

Table 6. Validation results of the ‘Red’ bambara groundnut landrace for final biomass (B) and yield (Y) [simulated (S) vs. Observed (O)] for field trials (FI and RF) and rainshelter experiments (30, 60, 100% ETa) conducted during 2011/12.

	Yield (t ha <sup>-1</sup> )									
	IRR		RF		30% <sup>w</sup> ETa		60% Eta		100% ETa	
	B	Y	B	Y	B	Y	B	Y	B	Y
<b>O</b>	12.14	2.84	8.75	1.84	7.41	0.35	8.61	0.32	8.11	0.52
<b>S</b>	11.84	2.37	8.81	1.80	4.56	0.52	7.84	0.91	9.51	1.14
<sup>x</sup> <b>RMSE</b>	0.30	0.47	0.06	0.04	2.85	0.17	0.77	0.59	1.40	0.62

<sup>w</sup>ETa – crop water requirement; <sup>x</sup>RMSE – root mean square error.



### *Validating taro*

Rainfed and irrigated treatments affected taro growth, biomass and yield significantly. The model was able to simulate CC under irrigated conditions very well ( $R^2 = 0.844$ ) (Fig 7A), although the model was not as accurate ( $R^2 = 0.018$ ) under rainfed conditions (Fig 7B). The model showed low RMSE, RMSEs and RMSEu for the full irrigation treatment under field conditions (Fig 7A), indicating good model performance. Consistent with the low  $R^2$  observed for rainfed conditions, model evaluation showed comparatively large RMSE, RMSEs and RMSEu under rainfed conditions, indicating poor model performance (Fig 7B). This may be due to the fact that the model was unable to simulate the sharp decline in CC that occurred in taro in response to stress. It must also be noted that unlike bambara groundnut, AquaCrop's default file for root and tuber crops may not be particularly suited to the unique growth pattern and behaviour of taro, an aroid. Parameters such as suckers/stolons and leaf appearance rate catered for in the simulating of underground bulking storage organs (SUBSTOR) aroid model (Singh *et al.*, 1998) as well as the crop's distinctive growth stages (Lebot, 2009) may need to be factored in the model for improved simulation of taro's canopy.

However, despite this setback, the model showed good prediction for biomass and yield under varying conditions. Figure 8 shows results of observed vs. simulated biomass and yield from field (RF and FI) and rainshelter (100, 60 and 30% ETa) experiments. The model was shown to simulate both biomass ( $R^2 = 0.898$ ) and yield ( $R^2 = 0.964$ ) relatively well with acceptably low values of RMSE, RMSEs and RMSEu. The agreement between simulated and observed biomass ( $d = 0.875$ ) and yield ( $d = 0.987$ ) was very good, which showed good agreement between predicted and observed values of biomass and yield (Fig 8). According to Jaleel *et al.* (2009), yield attainment is the most important attribute in crop production. As such, with regard to simulating yield response to water availability, the model's performance was good.

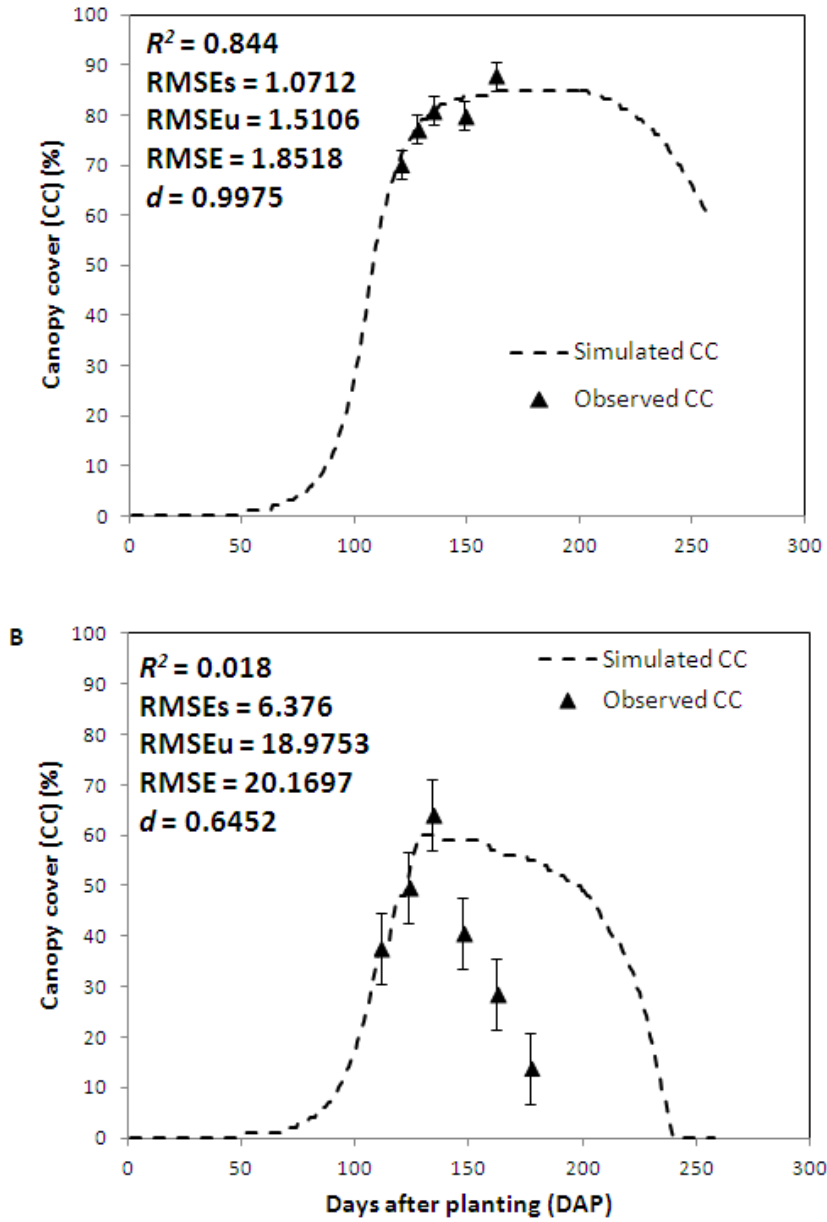


Figure 7. Validation of canopy cover (CC %) for taro grown under A. Irrigated and B. Rainfed field conditions during 2011/12 growing season at Ukulinga, Pietermaritzburg. Vertical bars indicate +/- standard error of means.

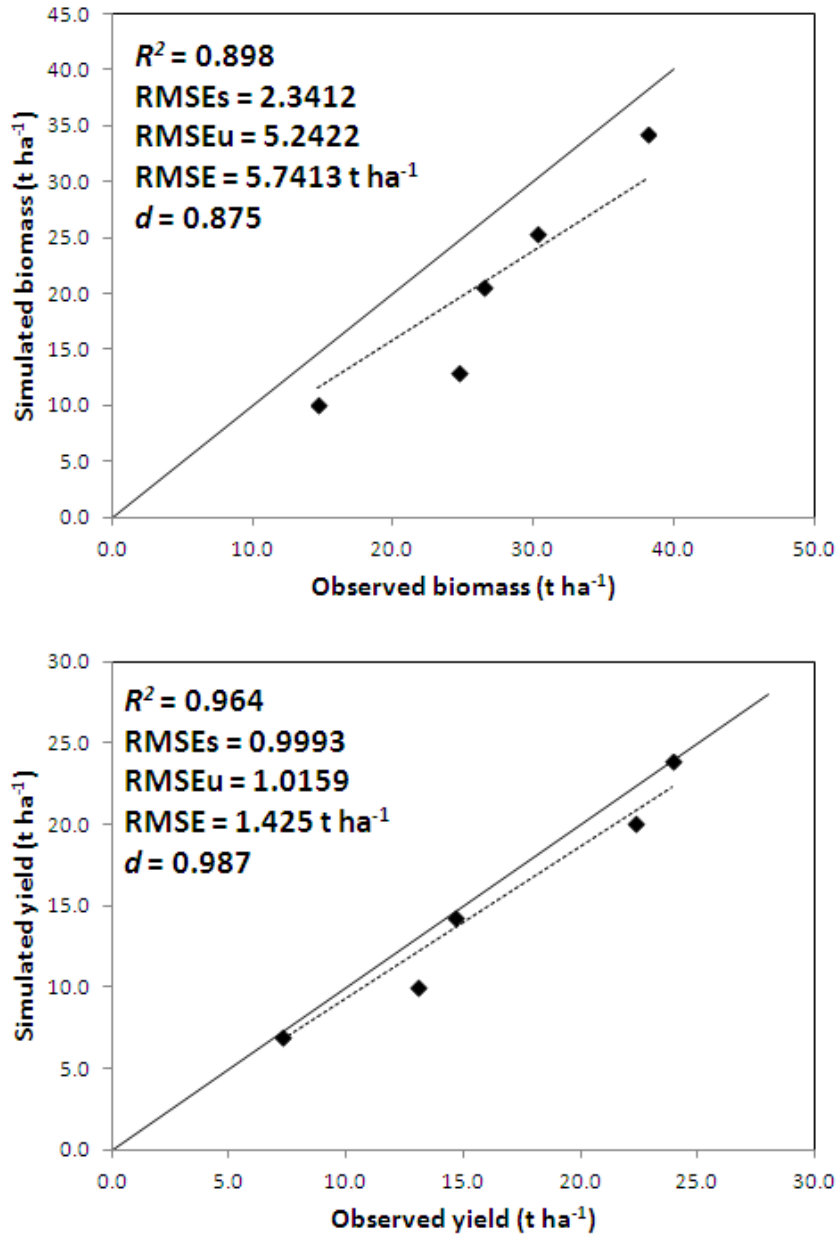


Figure 8. Validation results of taro final biomass and yield (t ha<sup>-1</sup>). Measured data are means from irrigated and rainfed field trials and rainshelter experiments (30, 60 and 100% ETa) grown during 2011/12 growing season at Ukulinga, Pietermaritzburg and Roodeplaat, Pretoria, respectively.

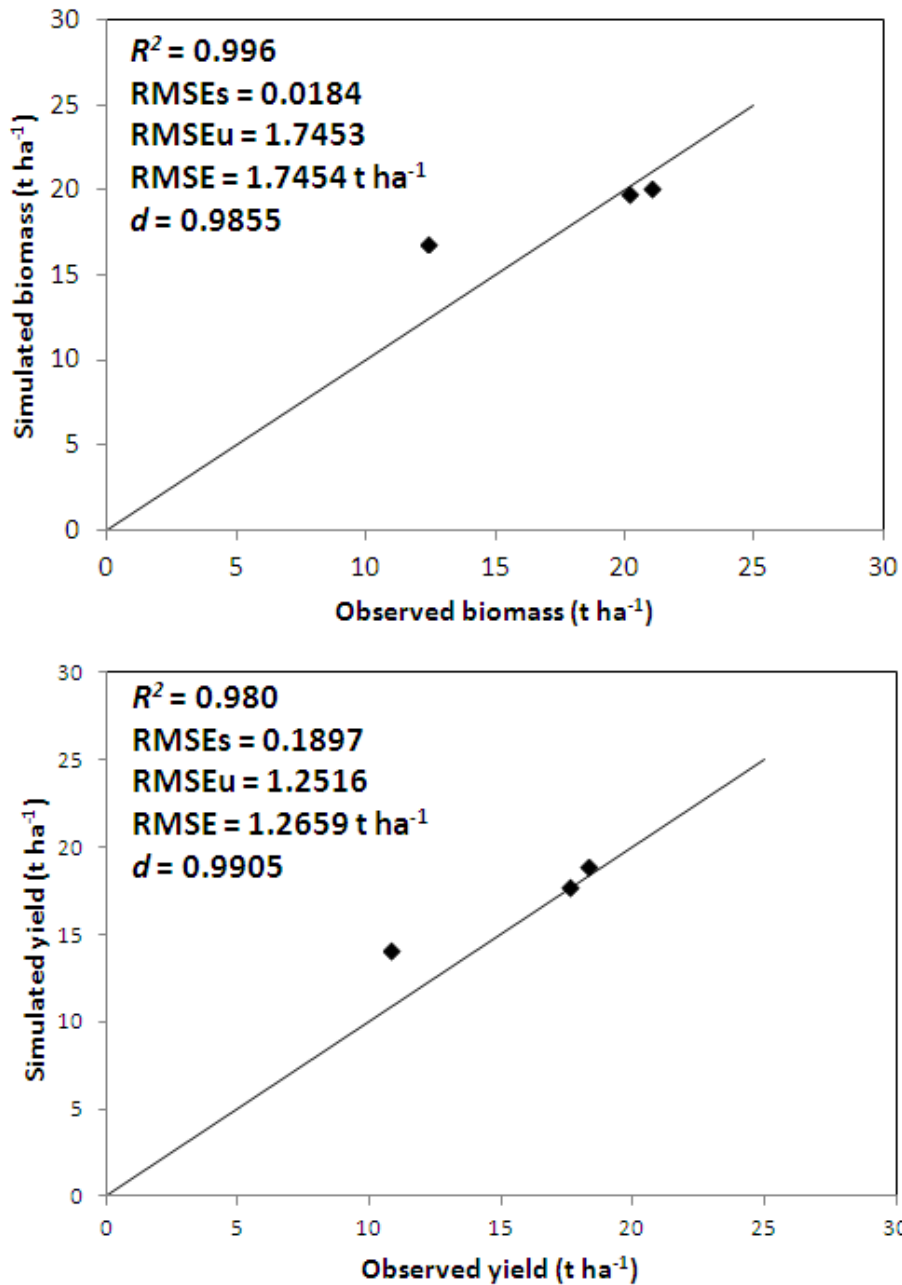


Figure 9. Validation results of taro biomass and yield (t ha<sup>-1</sup>) using independent data set for taro (Mare and Modi, 2009).

Validation of the model using results from independent experiments gave a very good fit for both biomass ( $R^2 = 0.996$ ) and yield ( $R^2 = 0.980$ ) (Fig 9). For interpretation of these results,  $R^2$  is dependent on the number of data points, where few data were used ( $5 \leq n \leq 3$ ),  $R^2$  has to be very high ( $R^2 = 0.99$ ) to show significance. Therefore,  $R^2$  of 0.99 and 0.98 for biomass and yield, respectively, for the 3 planting dates implies a significant regression. The agreement (*d-index*) between simulated and observed values of biomass and yield was respectively, 0.9855 and 0.9905 (Fig 9), showing very good agreement between predicted and observed values. In addition, RMSE was shown to be very low. The RMSEs were shown to approach zero for simulations of biomass and yield (Fig 9). This shows very good model performance and prediction given that this was an independent data set under dryland (rainfed) conditions. This further strengthens the model's applicability to simulating rainfed or water-limited production.

## CONCLUSIONS

While bambara groundnut has recently been calibrated in AquaCrop, the calibration and validation of taro was a first. The calibration and validation of AquaCrop for bambara groundnut gave good results, especially under field conditions. Final simulation of biomass and yield under field conditions (RF and FI) was satisfactory. However, due to great variability within landraces, more research needs to be done to further test the model for bambara groundnut landraces from other locations. This may also aid in selection and screening for drought tolerance in bambara groundnut. With regards to taro, the model simulations for biomass and yield were very satisfactory. Despite the model's obvious challenges in simulating canopy cover under rainfed conditions, the model was able to simulate final biomass and yield reasonably well. Given the unique nature of taro growth, more research needs to be done, together with possible improvements to the model, to better simulate taro growth. To fine-tune the model for taro, improvements should consider the crop's distinctive growth stages, pattern of yield formation as well sensitivities to frost which typically kills off the crop which would otherwise be a perennial. The model's minimal requirements for site specific information and crop input parameters for AquaCrop added to the ease of calibration and validation of the model – this is particularly beneficial within the

greater and broader context of encouraging the adoption of models as decision making support tools in places where access to extensive data sets may be limited. Over-all, the model showed that the taro Umbumbulu landrace and 'Red' bambara groundnut landrace selection are possible drought tolerant crops. This was evidenced by the model's ability to simulate both crops under water-limited conditions (30% ETa) and the crops' ability to achieve reasonable yields under such conditions. The continuing efforts to model bambara groundnut and this first attempt to model taro should be used as a stepping stone for modelling other neglected underutilised crops.

*Acknowledgements.* Water Research Commission of South Africa K5/177/4 Water-Use of Drought Tolerant Crops. WRC Knowledge Review 2008-09.

### **References**

**(See final references list pages 198-228)**

## GENERAL DISCUSSION

The water-energy-food security nexus dominates debates about world economic development in response to modern challenges. This debate has to take place in the context of the need to conserve biodiversity. The combination of water scarcity, predicted climate change and increasing population that our world is facing has painted a gloomy picture of future food security for countries like South Africa that already have scarce water resources (RSA, 1998). The impending threat has led to previously neglected and underutilised species/crops (NUS) being touted as possible future crops. However, decades of ‘neglect’ by researchers and farmers in favour of major crops have meant that there currently exists limited information describing agronomy and water-use of NUS. This study hypothesised that local taro (*Colocasia esculenta* L. Schott) and bambara groundnut (*Vigna subterranea* L. Verdc) landraces may have acquired drought tolerance over years of natural and farmer selection under often harsh conditions. It was further hypothesised that such drought tolerance, in bambara groundnut, may be associated with seed coat colour. To test these hypotheses, conventional field experimentation and modelling approaches were adopted. These included experiments evaluating the effect of water stress on local taro and bambara groundnut landraces, alternative cropping systems and modelling yield responses of local taro and bambara groundnut landraces to water availability.

### ***Drought tolerance***

The importance of good crop establishment in crop production can never be over-emphasised. It allows for good root and early canopy development (Passioura, 2006; Blum, 2012) as well as maximum crop stand. This study showed that taro and bambara groundnut landraces were slow to emerge, on average they took 49 and 35 days after planting, respectively, to emerge (Chapters 3-6; Mabhaudhi *et al.*, 2011, 2012). This was slower than reported emergence in similar root/tuber and grain legume crops. Poor crop establishment can have deleterious effects to which no amount of effort or expense later in the season can resolve (Mabhaudhi

and Modi, 2011). Slow establishment also implies that a lot of water is lost to evaporation during early season as opposed to transpiration which is productive as it goes via the plant.

For bambara groundnut, there was an added hypothesis of the effect of seed colour on crop establishment. This emanated from previous studies (Mabhaudhi and Modi, 2010, 2011; Mbatha and Modi, 2010; Zulu and Modi, 2010) that have suggested an association between dark coloured seeds and seed quality. Results of this study failed to reject this null hypothesis. The 'Red' bambara groundnut landrace selection showed better emergence than its lighter coloured selections (Chapters 5, 6; Mabhaudhi *et al.*, 2011). The association between seed coat colour and drought tolerance may be linked the phenols which confer dark colour. Phenolic compounds are also known to have antioxidant properties which may be useful during stress acclimation. Although this does not take away the broader implications of slow establishment, it suggests that seed coat colour may be a useful selection criterion for improved vigour in bambara groundnut.

Stomatal closure is widely accepted as the primary limiting factor to photosynthesis and consequently yield under water limited conditions (Chaves *et al.*, 2002, 2003). Results from this study showed a trend of lower stomatal conductance under water limited relative to optimum conditions for both taro and bambara groundnut landraces (Chapters 3-6; Mabhaudhi *et al.*, 2012). The extent of such reductions was landrace specific. For taro, one upland landrace – Umbumbulu (Chapter 2) – showed greater stomatal regulation compared to two other landraces – the wild Dumbe Lomfula and semi-domesticated KwaNgwanase – which are both normally cultivated in shallow rivers and swamps, respectively (Chapter 2). These two landraces may be adapted to higher levels of water-use than the Umbumbulu landrace which is cultivated upland. The adaptability of upland taro varieties has also been observed and reported on by Uyeda *et al.* (2011). The 'Red' bambara groundnut landrace selection also showed greater stomatal regulation relative to the 'Brown' and 'Light-brown' landrace selections, further strengthening the association between seed colour, seed quality and possible drought tolerance. The degree of stomatal regulation observed in the Umbumbulu taro landrace and 'Red' bambara groundnut landrace selection implies an ability to reduce water-use through reduced transpiration losses, an adaptation associated with drought avoidance mechanisms (Levitt, 1972). There are, however, schools of thought that argue against this



mechanism as not being beneficial to yield attainment (Blum, 2005, 2009). They argue that any drought adaptation strategy that lowers stomatal conductance, which is directly linked to biomass and yield, is to the detriment of yield attainment. They suggest that, instead, drought adaptation should be linked with crops that maintain their high levels of transpiration while enhancing soil water capture.

Limitations to photosynthesis under stress have also been attributed to metabolic impairment (Lawson *et al.*, 2003). This includes protein denaturation, accumulation of free radicals and loss of pigments (chlorophylls and carotenoids) (Farooq *et al.*, 2009). It was within this context that chlorophyll content was evaluated as an index for evaluating drought tolerance of taro and bambara groundnut landraces. The expectation was that under water limited conditions chlorophyll content would decrease as a strategy to down-regulate the rate of photosynthesis in response to lower intracellular CO<sub>2</sub> availability owing to stomatal closure. Results for taro and bambara groundnut landraces showed lower chlorophyll content index under water limited conditions (Chapters 3-5). The taro Umbumbulu landrace and 'Red' bambara groundnut landrace selection showed this adjustment better than the other landraces used in the study. This suggests that the two landraces are capable of down-regulating their photosynthesis under water limited conditions, an adjustment that may also help to control accumulation of free radicals caused by an excess of excited electrons (Farooq *et al.*, 2009). These results showed that chlorophyll content index may be a useful index for assessing drought tolerance. However, more studies are needed for this trait since observations of chlorophyll content index were only conducted during the 2011/12 growing season. Reduction in chlorophyll content, the chief light-harvesting pigment, also implies energy dissipation as a stress tolerance mechanism.

For the taro Umbumbulu landrace, other responses such as leaf rolling and heliotropism as well as partial senescence of the leaf under water limited conditions were also observed. Leaf rolling and partial senescence of the leaf may be related to minimising transpirational losses by directly reducing surface area available for transpiration. Alternatively, leaf rolling could be related to lower energy absorption, hence reduced transpiration. Leaf heliotropism is related to energy dissipation – typically, the adaxial surface, which contains less chlorophyll and is therefore lightly coloured relative to the abaxial surface, would be turned upwards towards the

sun while the abaxial surface would face downward away from the sun. Leaf heliotropism is also a complimentary strategy to loss of chlorophyll. Hypothetically, such a mechanism would allow for reflection of radiation, cooling of the leaf surface as well as contributing towards reduced transpiration, traits synonymous with drought avoidance.

The literature review (Chapter 1) showed that there are three drought tolerance mechanisms – avoidance, escape and (desiccation) tolerance (Levitt, 1972). Two of these (avoidance and escape) are intricately linked to crop canopy size and characteristics. As such, the study placed emphasis on measurements related to crop canopy (plant height, leaf number and leaf area index). This was also linked to a secondary objective of the study related to modelling taro and bambara groundnut. Briefly, smaller canopy size is a function of drought avoidance (Levitt, 1972). Although drought escape is often related to crop phenology, it is also associated with crop canopy characteristics in that smaller canopy size and reduced crop duration will often translate to a shorter growth cycle. The specifics of these mechanisms and how they interact in bambara groundnut and taro landraces are discussed below.

This study showed that crop canopy size was sensitive to water limited conditions. Both taro and bambara groundnut landraces showed reduced canopy size under water limited conditions (Chapters 3 – 6; Mabhaudhi *et al.*, 2011, 2012). However, since crop canopy size is directly related to biomass accumulation and yield attainment, there should be a balance between minimising water losses through transpiration and biomass production which is a function of transpiration (Chapter 1; Raes *et al.*, 2009; Steduto *et al.*, 2009). Thus, in this regard, the taro Umbumbulu landrace and ‘Red’ bambara groundnut landrace selection which showed moderate reduction in growth may be regarded as being adapted to water limited conditions.

A vegetative growth index (VGI) was also computed for taro landraces and used to evaluate crop responses to limited water availability under rainfed conditions (Chapter 3). The VGI is particularly useful in that it encompasses all the components of taro’s vegetative growth i.e. leaf number and area, plant height as well as stolons and/or suckers (Lebot, 2009). The VGI showed that while vegetative growth of all taro landraces was negatively affected by limited water availability, the Umbumbulu landrace was least severely affected than the Dumbe Lomfula and KwaNgwanase landraces under rainfed conditions. This was consistent

with the Umbumbulu landrace's moderate canopy size and further suggested it as being adapted to water limited conditions. Therefore, the VGI is a useful index for drought tolerance studies in taro.

Bambara groundnut landrace selections displayed a degree of phenological plasticity associated with drought escape under water limited conditions by flowering and maturing earlier as well as shortening the duration of the flowering period (Chapters 5 and 6). Drought escape in bambara groundnut was related to lower leaf number and shorter crop canopy duration resulting from enhanced canopy senescence under water limited relative to optimum conditions. The downside to drought escape, however, is that there is less time for build-up of harvest index (yield formation) translating to lower yields. This was evident with yield losses of up to 50% observed in bambara groundnut landrace selections under water limited relative to optimum conditions. Nonetheless, the positive side to drought escape is that it ensures attainment of "some" yield as opposed to no yield at all in the event that water stress was terminal. This is of particular importance to farmers in marginal areas of crop production where crops would fail many years. The 'Red' landrace selection showed delayed leaf senescence under water limited conditions, a phenomenon also observed in cowpea (Odindo, 2007). This may explain the 'Red' landrace selection's ability to produce reasonable yields under water limited conditions.

Taro landraces also showed phenological plasticity in that landraces generally matured earlier under water limited relative to optimum conditions. Early maturity was closely related to low leaf number associated with enhanced leaf senescence under water limited conditions. This was quite evident in the Umbumbulu landrace (Chapter 3). Drought escape may be a desirable trait in taro. This is because if the crop did not mature early (i.e. escape drought) it would result in the possible re-translocation of assimilates from the underground storage organ (corm and cormels) to above-ground parts resulting in yield losses. Therefore, the Umbumbulu landrace which exemplified phenological plasticity under water limited conditions may be regarded as being adapted to water limited conditions.

Finally, the purpose of crop production is to produce yield (Jaleel *et al.*, 2009). Yield of taro and bambara groundnut landraces was generally lower under water limited conditions compared with optimum conditions. Such yield adjustment could be linked to taro and

bambara groundnut's drought tolerance mechanisms as suggested during assessments of yield components. Correlation and path analysis of yield determinants for both crops showed that biomass was highly correlated to yield and had the greatest contribution to yield. Ironically, drought avoidance and escape mechanisms observed in both crops were at the expense of biomass accumulation owing to reduced transpiration and photosynthesis rates as well as smaller canopy size and duration. This concurs with Blum's (2005, 2009) reports that drought avoidance and escape as well as increased water-use efficiency were often at the expense of yield attainment. However, Blum (2011) also stated that effective drought tolerance in crops was mostly achieved through drought avoidance. Therefore, through drought avoidance and escape, taro and bambara groundnut landraces were able to achieve reasonable yields under water limited conditions. Moreover, the taro Umbumbulu landrace and 'Red' bambara groundnut landrace yielded above normal mean yields reported for each crop under dryland conditions (Swanevelder, 1998; FAOSTAT, 2012).

Another interesting observation was that of improved water productivity in taro landraces grown in rainshelters compared to field conditions (Chapters 3 and 4). The use of drip irrigation in rainshelters resulted in a smaller wetted surface which translated to reduced soil evaporation losses. Additionally, frequent scheduling of irrigation, and therefore constant re-wetting of the root zone, may be beneficial to taro which is typically a shallow rooted crop. Thus, even at low water regimes [30% of crop water requirement (ET<sub>a</sub>)] the crop was still able to access water within its root zone and achieve yield similar to that achieved under rainfed production. This showed that the use of drip irrigation may not only reduce overall crop water-use, but also improve yields.

### ***Intercropping***

Another objective of this study was to evaluate the agronomic performance of intercropping taro and bambara groundnut landraces under dryland conditions (Chapter 7). Typically, both crops are cultivated as sole crops under dryland conditions with taro being more dominant in terms of land allocation in KwaZulu-Natal. Results showed that there is much potential for intercropping taro and bambara groundnut. An evaluation of intercrop productivity using the land equivalent ratio (LER) showed that intercropping taro and bambara groundnut at ratios of

1:1 (taro:bambara groundnut) and 1:2 was more productive than cultivating either taro or bambara groundnut as sole crops. On average, over the two growing seasons, the 1:1 intercrop had a LER of 1.53 compared with 1.23 for the 1:2 intercrop. Under future climate conditions, choice of cropping system will also play a major role in ensuring food security. Therefore, re-introducing and promoting cropping systems such as intercropping may offer farmers in semi-arid rural areas greater resilience under conditions of predicted climate as well as a safer and possibly more lucrative alternative to sole cropping (Reithman *et al.*, 2007).

### ***Modelling yield response of taro and bambara groundnut to water availability***

Data collected from pot, field and rainshelter experiments was used to develop crop inputs to calibrate and validate the FAO's AquaCrop model for taro and bambara groundnut landraces. The taro Umbumbulu landrace and the 'Red' bambara groundnut landrace selection were selected for modelling. Their selection was based on observations from experiments that showed them to be stable and adaptable to water limited conditions. Model performance was evaluated using the coefficient of determination ( $R^2$ ), root mean square error (RMSE) and its components (RMSEs and RMSEu) as well as Willmott's (d) index of agreement.

Taro calibration showed that AquaCrop predicted canopy cover (CC) reasonably well ( $R^2 = 0.789$ ;  $d\text{-index} = 0.9196$ ). Simulation of final biomass and yield was satisfactory and showed very good fit for predicted and observed data. Validation using data from rainfed and irrigated field trials showed good model performance for CC under irrigated conditions ( $R^2 = 0.844$ ;  $d\text{-index} = 0.9975$ ). However, the model was not as accurate ( $R^2 = 0.018$ ;  $d\text{-index} = 0.6452$ ) under rainfed conditions. Nonetheless, the model showed good prediction for taro biomass ( $R^2 = 0.898$ ;  $d\text{-index} = 0.875$ ) and corm yield ( $R^2 = 0.964$ ;  $d\text{-index} = 0.987$ ) under all conditions (field and rainshelters). Validation performed using independent taro data showed very good fit for both predicted and observed biomass ( $R^2 = 0.996$ ;  $d\text{-index} = 0.9855$ ) and yield ( $R^2 = 0.980$ ;  $d\text{-index} = 0.9905$ ). This was considered to be very good given that this was a first attempt to simulate a taro landrace using AquaCrop.

Calibration results for the bambara groundnut landrace showed good fit between predicted and observed values for CC ( $R^2 = 0.94$ ;  $d\text{-index} = 0.989$ ) and biomass ( $R^2 = 0.957$ ;  $d\text{-index} =$

0.998) as well as low RMSE, implying good model performance. Simulation of final biomass and yield showed good comparison between predicted and observed biomass and yield. Model validation using data from field experiments showed good fit between predicted and observed CC under irrigated ( $R^2 = 0.858$ ;  $d\text{-index} = 0.9558$ ) and rainfed conditions ( $R^2 = 0.951$ ;  $d\text{-index} = 0.9746$ ). The RMSE for CC was relatively low (9.717 and 6.176%) indicating ‘good’ model performance and robustness. Model validation using data from rainshelter experiments showed good fit between predicted and observed CC under the varying water regimes – 100% ETa ( $R^2 = 0.972$ ;  $d\text{-index} = 0.972$ ), 60% ETa ( $R^2 = 0.951$ ;  $d\text{-index} = 0.951$ ) and 30% ETa ( $R^2 = 0.950$ ;  $d\text{-index} = 0.950$ ). The model predicted final biomass and yield very well for field trials with a low margin of error, which is indicative of good model performance. However, the model under-estimated CC for the early and later parts of the season and over-estimated final biomass and yield in the rainshelter. Model performance in the rainshelter was possibly negatively affected by periodic closing and opening of the shelter during rainfall events. This could have increased radiation and possible reduced wind speed in the rainshelter – a phenomenon that would also explain the low harvest index observed in bambara groundnut grown in rainshelters (Chapter 6).

Over-all, for taro and bambara groundnut landraces, the model predicted biomass and yield well under field conditions; this was especially true for bambara groundnut under rainfed conditions. This concurred with reports by Raes *et al.* (2009) and Steduto *et al.* (2009) that the model was particularly useful for predicting yield under water-limited conditions.

## CONCLUSIONS

The study successfully indexed drought tolerance strategies in taro landraces as involving a combination of drought avoidance and escape mechanisms. Drought avoidance was achieved through stomatal regulation, energy dissipation (loss of chlorophyll and heliotropism) and smaller canopy size resulting in lower crop water losses to transpiration. Drought escape was demonstrated through phenological plasticity – under water limited conditions as taro matured earlier. Yield was lower in response to limited water availability while WUE remained relatively unchanged across water treatments. The Umbumbulu landrace showed adaptability to production under water limited conditions. Relative to the Dumbe Lomfula and KwaNgwanase landraces, the Umbumbulu showed a greater degree of stomatal regulation, moderation in canopy size and duration, energy dissipation as well as minimal yield losses under water limited conditions. The Umbumbulu landrace had high WUE and may be suited to cultivation in areas with limited water availability. The significance of the Umbumbulu landrace's adaptability to water limited conditions suggests that breeding for drought tolerance in taro is a possibility.

Effective drought tolerance in bambara groundnut landrace selections was achieved through drought avoidance and escape mechanisms. Bambara groundnut landrace selections avoided drought by regulating water loss through stomatal closure and reducing canopy size thereby using less water and increasing WUE under conditions of limited water availability. Drought adaptation strategies at the canopy level were complemented by loss of chlorophyll – a heat dissipation strategy associated with drought avoidance. Bambara groundnut landrace selections showed phenological plasticity under limited water availability – flowering was hastened, flowering duration was shorter, leaf senescence was enhanced resulting in shorter crop duration and consequently early maturity. This resulted in lower seed yield through less biomass and lower harvest index, lower pod number and mass. However, bambara groundnut landraces produced reasonable yields under limited water conditions – suggesting that they are suitable for cultivation in semi-arid and marginal areas of agricultural production.

Seed colour in bambara groundnut had an effect on crop establishment. The 'Red' and 'Brown' landrace selections emerged better than the 'Light-brown' landrace selection. This

implies that seed colour can be a possible selection criterion for improved growth vigour in bambara groundnuts. In addition, the 'Red' bambara groundnut selection showed greater stomatal regulation relative to the 'Brown' and 'Light-brown' landrace selections. This further suggests an association between seed colour and drought tolerance in bambara groundnuts. Therefore, seed coat colour may be a useful initial selection criterion for improved vigour and possible drought tolerance in bambara groundnut.

Simultaneous intercropping of taro and bambara groundnut is more productive compared to sole crops of either crop. The 1:1 (taro:bambara groundnut) intercrop had a LER of 1.53 compared to 1.23 for the 1:2 intercrop, indicating there was an advantage to intercropping. In addition, intercropping taro and bambara groundnut at a ratio of 1:1 had no negative effect on growth of either taro and bambara groundnut landraces. Intercropping taro with bambara groundnut was shown to be highly productive, in terms of additional output per unit area of land accrued from bambara groundnut. Intercropping taro with bambara groundnut also showed no significant negative effect on yield of taro as the main crop. Inclusion of bambara groundnut (a legume) in taro cropping systems may be complimentary in that improves the overall water-use of the farming system through greater capture of water in the horizon. Furthermore, the fact that taro and bambara groundnut roots extract water from different depths of the soil profile would imply reduced drainage losses. Therefore, intercropping taro with bambara groundnut is productive, sustainable and beneficial in that it has potential to improve farmers' nutritional productivity per unit area, bolster food security and enhance resilience of farmer's cropping systems.

Calibration and validation of the FAO's AquaCrop crop model for taro and bambara groundnut landraces was successful and gave satisfactory results, particularly under field conditions. The model was able to simulate canopy cover for both crops under varying conditions reasonably well. However, there were challenges in simulating canopy cover for taro, especially under rainfed conditions. This was acceptable given the unique vegetative growth pattern of taro – an aroid – which is not expressly catered for in the model. However, for both crops, the model predicted final biomass and yield with acceptable accuracy. Evaluation of model performance showed good performance most of the time. The model's demonstrated ability to simulate yield response to water would make it a useful tool in



selecting and screening for drought tolerance in taro and bambara groundnut landraces as well as for several other NUS. This would aid in the quest to generate information databases describing the agronomic performance and water-use of these crops. Furthermore, AquaCrop's minimal input requirements and ease of calibration and validation would make it a particularly useful tool in this regard. This study's effort to model bambara groundnut and the first attempt to model taro in AquaCrop should serve to encourage modelling of other neglected underutilised crops.

## RECOMMENDATIONS

The following recommendations may be made, based on observations made during the study;

- Given the importance of vigorous and uniform emergence, strategies to improve emergence of both taro and bambara groundnut should be a key objective of any future studies. For bambara groundnut, such research may focus on priming methods that have previously been used to improve crop establishment in other crops. With regards to taro, the use of head-sets or 'huli' as planting material may be an alternative to using corms.
- In addition, there is a need to evaluate the effect of water stress on nutritional composition and quality of taro corms and bambara groundnut grain. Such a study may also include effect of water stress on postharvest shelf-life of taro.
- The review of literature showed that in addition to morphological and eco-physiological adaptations, plants also respond to stress at a molecular level. Therefore, future research should investigate physiological responses of taro and bambara groundnut to water stress, focussing on compatible solutes, proteins and antioxidant activity.
- Any future study on drought tolerance of taro should include more landraces and, if possible, an introduced foreign genotype.
- Intercropping of taro and bambara groundnut was shown to be productive and to have minimal effect on taro yields. Therefore, it should be encouraged as an alternative cropping system in rural areas where taro is the dominant crop cultivated in sole cropping systems. Future research should also focus on the interaction between taro and bambara groundnut as a legume, with a view to establishing whether taro may benefit from nitrogen fixed by bambara groundnut.
- Further research is required to fine-tune the results of preliminary calibration and validation of taro using AquaCrop. Such an effort would result in a refined model that could then be made accessible to policy makers, extension workers and other researchers. The ease of using the model makes it a potential tool for extension and teaching.

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