

**MODELLING THE RESPONSE OF BAMBARA
GROUNDNUT (*Vigna subterranea* (L.) Verdc)
FOR ABIOTIC STRESS**

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LIST OF SYMBOLS AND ABBREVIATIONS

$f(\theta_{d(i)})$	function relating to photoperiod
%	percent
$^{\circ}\text{C}$	Celsius
a, b, c	landrace coefficients for leaf number function
A_d	phenochrones
BD	soil bulk density (g cm^{-3})
cm	centimetre
<i>coldstress</i>	cold stress due to low temperature
d	day
DAS	days after sowing
<i>DEADLW</i>	dead leaf weight ($\text{g m}^{-2} \text{ day}^{-1}$)
<i>density</i>	number of plants per square meter
<i>Densityfac</i>	density factor
DL	daylength in hours
DL_{fac}	daylength factor
DR_i	drainage in layer i (mm d^{-1})
E	water capture parameter
Eq.	equation
$EVAP_{pot}$	potential evaporation (mm d^{-1})
F_{Leaf}	daily fraction of leaf
F_{Roots}	daily fraction of roots
F_{Stem}	daily fraction of stem
FC	field capacity (mm)
FC_{layer}	the soil moisture at field capacity in layer i (mm)
Frs	recoverable fraction of assimilates per day
g	gram
G_{actual}	actual growth rate ($\text{g m}^{-2} \text{ da}^{-1}$)
h	hour

ha	hectare
<i>HI</i>	harvest index
HT	high temperature (33±5 °C)
<i>k</i>	light extinction coefficient
k Pa	kilo Pascal
kg	kilo gram
<i>KS₁</i>	stress index 1 (leaf appearance)
<i>KS₂</i>	stress index 2 (leaf senescence)
<i>KS₃</i>	stress index 3 (dry matter partitioning)
<i>k_w</i>	‘root water capture coefficient’ (cm ²)
<i>LA</i>	leaf area (cm ² plant ⁻¹)
<i>LA_l</i>	landrace parameter for leaf area
<i>LAI</i>	leaf area index
<i>LLG</i>	light limited (g m ⁻² day ⁻¹)
<i>LN</i>	actual leaf number day ⁻¹
<i>LN_{dead}</i>	dead leaf number day ⁻¹
<i>LN_{new}</i>	new leaf number day ⁻¹
LT	low temperature (23±5 °C)
<i>L_v</i>	root length density (cm cm ⁻³)
<i>LW</i>	leaf weight (g m ⁻² day ⁻¹)
<i>M</i>	measured value
m	meter
<i>MAE</i>	mean absolute error
MJ	mega joule
mm	millimeter
n	number of days experienced by the crop since sowing
<i>N_i</i>	total number of leaves (plant ⁻¹)
<i>N_{ph}</i>	number of accumulated phenochrons
<i>N-S</i>	The Nash and Sutcliffe Model Efficiency Measure
<i>P₀</i>	Phenological time from sowing to emergence
<i>P_l</i>	landrace parameter for daylength factor

P_1	Phenological time from emergence to end of juvenile period
P_2	phenological duration of the inductive period
P_3	phenological time from emergence to flowering
P_4	phenological time from flowering to podding
P_5	phenological time for pod maturity
P_6	phenological duration from maturity to harvest
$PanE$	pan evaporation (mm d^{-1})
PAR	photosynthetically Active Radiation
p_i	phyllochron (number of leaves plant^{-1} phenochron $^{-1}$)
PN	number of pods produced (number of pods $\text{plant}^{-1} \text{ day}^{-1}$)
PW	weight of individual pod ($\text{g pod}^{-1} \text{ day}^{-1}$)
PWP	permanent wilting point (mm)
RW	root weight ($\text{g m}^{-2} \text{ day}^{-1}$)
RWC	relative water content
s	second
S	simulated value
SAT	saturation capacity (mm)
SD	saturation deficit ($\text{g kg}^{-1} \text{ kPa}^{-1}$)
SE	standard error
$SeedReLoc$	relocation of assimilates from seed ($\text{g m}^{-2} \text{ d}^{-1}$)
$SEEDW$	individual seed weight ($\text{g m}^{-2} \text{ day}^{-1}$)
Sen_L	senescence fraction due to mutual shading
Sen_{PHY}	senescence fraction due to physiological maturity of leaves
Sen_T	senescence fraction due to temperature stress
Sen_W	senescence fraction due to water stress
S_i	short wave solar radiation (MJ day^{-1})
SLA	specific leaf area
S_t	transmitted radiation (MJ day^{-1})
$STEMW$	stem weight ($\text{g m}^{-2} \text{ day}^{-1}$)
T_{lower}	lower threshold level of temperature ($^{\circ}\text{C}$)
T_{upper}	upper threshold level of temperature ($^{\circ}\text{C}$)
t	tons

TCRU	Tropical Crops Research Unit
$TCRU_{density}$	plant density in TCRU experiment (15 plants m ⁻²)
$T_{d(i)}$	hourly temperature in hour i (°C)
TDM	total dry matter
TE	transpiration efficiency (g mm ⁻¹)
T_{high}	ceiling temperature
T_{max}	daily maximum temperature
T_{mean}	daily mean temperature
T_{min}	daily minimum temperature
$T_{opt,}$	optimum temperature
$Total$	daily sum of partitioning fractions (1)
$TSTRESS$	temperature stress index.
TT	cumulative thermal time (degree days)
ΔTT_i	daily thermal time (degree days d ⁻¹)
U_{actual}	actual rate of water uptake by roots in profile (mm d ⁻¹)
UP_i	actual rate of water uptake by roots in layer i (mm d ⁻¹)
$U_{pot(i)}$	rate of change in potential water uptake in layer i (cm d ⁻¹)
$U_{pot(soil)}$	potential rate of water uptake by roots in profile (mm d ⁻¹)
$WATER_i$	rate of change in soil moisture in layer i (mm d ⁻¹)
WLG	water limited growth
WM_1	water factor 1
WM_2	water factor 2
$WSTRESS$	water stress index
Y	fraction of root system accumulated from soil surface
Y_d	cumulative fraction of roots at depth d
Y_{d-10}	cumulative root fraction at depth ($d-10$)
Y_{ield}	the end-of season yield (kg ha ⁻¹ y ⁻¹),
β	parameter to describe root distribution with depth
β_1	value of beta at early growth stage
β_2	power of increasing β with accumulation of thermal units
ε_s	efficiency of conversion of radiation into biomass (g MJ ⁻¹)

ε_{water}	water conversion efficiency into biomass (g MJ^{-1})
θ	fraction of available water in soil layer
λ	landrace coefficient ($\text{cm}^2 \text{ plant}^{-1} \text{ phenochron}^{-1}$)
σ	specific root weight (g km^{-1})
ψ_w	water potential

ABSTRACT

Bambara groundnut (*Vigna subterranea* (L.) Verdc) is an indigenous legume that is still cultivated in subsistence agricultural systems in sub-Saharan Africa, despite the lack of any major research effort until recently. The crop is cultivated from local landraces as there are no true varieties of the species bred for specific traits. The variable and hostile climates in the region mean that annual yields of most rainfed crops including bambara groundnut are far below their agronomic or genetic potential. The lack of quantitative information on the eco-physiological responses of the crop to various abiotic factors has resulted in poor decision making on crop management practices especially in relation to sowing date and the selection of appropriate landraces for different locations. Modelling of bambara groundnut was initiated previously but there is still insufficient understanding of how growth and developmental processes can be simulated under abiotic stress and different photoperiods. The aim of this study was to develop a crop simulation model for bambara groundnut to predict growth, development and yield under drought, heat and cold stress and different daylengths.

The present model (BAMGRO) is an adaptation of the established CROPGRO and previous bambara groundnut models; BAMnut and BAMFOOD project model. It uses climate data, landrace specific parameters and soil characteristics and runs on a daily time-step to determine the canopy development, biomass production and yield of a landrace in a specific environment. The parameters of the model have been determined with glasshouses data (TCRU, University of Nottingham) and published information. BAMGRO is capable of describing differences between landraces, and the influence of drought, temperature and photoperiod using a simplified approach.

The present modelling approaches with BAMGRO model provide useful predictive information on canopy development, biomass production and yield formation of bambara groundnut landraces under contrasting environments. Two contrasting landraces; Uniswa Red (Swaziland) and S19-3 (Namibia) were used in

the present study to evaluate the growth and yield performances under drought, heat and cold stress.

BAMGRO has been primarily validated against independent data sets of two years glasshouse for two contrasting landraces; Uniswa Red and S19-3 grown under two temperatures (23 ± 5 °C, 33 ± 5 °C) with drought. Further, it was validated for field data in Botswana with two sowing dates (January 18, February 1) during the 2007 season and for Swaziland for three landraces; Uniswa Red, DipC, OM1. The model achieves a good fit between observed and predicted data for *LAI* (Nash and Sutcliffe (N-S), 0.78-0.98; Mean Absolute Error, ± 0.14 -0.57) for tested four landraces. Pod yield simulation was correlated well with measured values especially for Uniswa Red and S19-3 (N-S 0.73-0.87; Mean Absolute Error ± 16 g m⁻²) while it was poor for DipC and OM1 (N-S, 0.46-0.50; Mean Absolute Error, ± 15.6 -17.7 g m⁻²). Further, the comparison of simulated and measured data of *TDM* reported lower correlation compared to *LAI* and yield. (N-S, 0.59-0.79; Mean Absolute Error ± 48 -100 g m⁻²) indicating overall underestimation. The performance of the BAMGRO-soil water module was tested by validating the available soil moisture and results indicating that it over estimated for upper layers while deeper layers showed lower prediction.

The possible reasons for the discrepancies in measured and simulated data are differences in quality and quantity of solar radiation in UK summer and Semi-arid Africa, intra-landrace variability and poor calibration of soil water module. Four potential applications of BAMGRO and three future developments are presented in this thesis.

CHAPTER 1

1. INTRODUCTION

The heuristic value of a crop model for determining growth and yield are well established (Sinclair and Seligman, 1996). Crop models have proved to be valuable tools for comprehensively synthesising quantitative understanding of physiological processes, hypothesising genetic manipulations and evaluating crop management strategies (Boote et al., 1996). Since the 1970's a stream of publications on crop modelling has been added to the literature comprising new models and updates or applications of earlier models. The broader goal of a crop model is to simulate and explain crop development, growth and yield as functions of environment, management and genetically controlled characteristics. Consequently research interest is focussed towards the manipulation of management practices; such as selection of a genotype for a specific environment and scheduling of irrigation and planting dates, to achieve the highest economic returns. A range of crop models have been developed for major crops where eco-physiological interactions are well established. However limited attempts have been made in modelling underutilised crops for which the general literature is sparse.

The detailed and extensive research project (BAMFOOD) at the University of Nottingham, UK and collaborative partners from various institutes in Africa (Botswana College of Agriculture (Botswana), University of Swaziland (Swaziland), and Ministry of Agriculture and Water Resources (Namibia)) have revealed the potential of bambara groundnut in marginal lands of semi-arid Africa where low input agriculture is normally practised.

Bambara groundnut (*Vigna subterranea* (L.) Verdc) is a legume with significance as a source of protein in sub-Saharan Africa where it is mainly grown by women

farmers for the subsistence of their families. Its nutritional composition (protein content is 16-25%) is highly comparable or superior to other legumes (Linnemann and Azam-Ali, 1993), providing an important supplement to cereal-based diets. It is mainly grown for its seeds and is eaten fresh when unripe and as a pulse when ripened and mature (Linnemann and Azam-Ali, 1993). In the absence of established varieties, marginal and subsistence farmers in Africa grow locally selected 'landraces' of bambara groundnut.

The production and consumption of bambara groundnut is mainly confined to semi-arid Africa where very low and erratic distribution of rainfall, losses through run-off, drainage and evaporation result in only a small proportion of available soil moisture for crop growth. According to Azam-Ali and Squire (2002), the agro-ecological niche of bambara groundnut is similar to that of millet and groundnut. This niche of bambara groundnut is based on the observations that it appears to be more tolerant of drought conditions than other legumes (Linnemann and Azam-Ali, 1993). In spite of the presumed drought tolerant capabilities of bambara groundnut, results reported by Collinson et al., (1996, 1997) suggested that canopy expansion, biomass production and yield are reduced under water limited conditions indicating drought stress on growth and development. Lower biomass under drought is partly a consequence of the restricted leaf area expansion resulted in lower radiation interception and partly attributed by the direct effect of low net photosynthesis through stomatal closure (Mwanamwenge et al., 1999). Thus the quantification of reduction in growth and yield of bambara groundnut landraces under water limited environments is essential to screen the drought tolerance of landraces.

Temperature variability is a yield determining factor in many parts of the world including semi-arid Africa where bambara groundnut is normally grown. The wide fluctuations in daily mean temperature in semi-arid Africa necessitate a thorough understanding of the effect of temperature stress on growth and development of bambara groundnut. In general, an increase in mean seasonal temperature of 2-4 °C reduces the annual yield of most determinate crops due to the shorter crop

duration (Wheeler et al., 2000) indicating heat stress. Also temperatures below the optimum accumulates relatively lower growing degree days resulting retardation of growth due to cold stress. However the exact mechanism of the effect of temperature stress on developmental processes and yield of bambara groundnut is unknown. The tolerance capacity of individual landrace determines the magnitude of the temperature effect on yield. Extremes of temperatures are a major constraint to crop adaptation and productivity; especially when they coincide with drought and critical growth stages of plant development (Prasad et al., 2000). The response of high temperature stress has been studied in detail for groundnut (Prasad et al., 2000), wheat (Ferris et al., 1998), cowpea (Ismail and Hall, 1999) and rice (Matsuie et al., 2001). Quantification of the temperature effect on growth and development provide pathways to minimise risk of bambara groundnut farming in Africa through matching existing landraces to suitable temperature conditions.

Bambara groundnut is a short day crop and both flowering and pod formation are affected by photoperiod (Haris and Azam-Ali, 1993; Linnemann, 1993; Brink, 1997). According to the linear model developed by Brink (1997) the thermal and photothermal rates of flowering and podding vary with the landrace. In particular photoperiod has a predominant role towards the rate of pod formation compared to flowering (Brink, 1997). Studies in other food legumes have reported that photoperiod mainly regulates the flowering and also the developmental phases beyond flowering for soya bean (*Glycine max*) (Grimm et al., 1994) and groundnut (*Arachis hypogaea*) (Flohr et al., 1990). However, quantitative information of the role of photoperiod on bambara groundnut landraces are limited and need further investigation.

To explore the potential growth and development of bambara groundnut landraces in various agro-ecological regions and to evaluate the possibilities of transferring them to different locations, it is vital to understand how crop processes are influenced by major environmental factors. Thus research work has prioritised the quantification of environmental factors through suitable modelling approaches.

The PARCH (Predicting Arable Resource Capture in Hostile Environment) based model (Collinson, 1996) was the first attempt to model bambara groundnut by evaluating agro-ecological potential. This model was based on very limited data sets from the first EU project (EU STD-3) in University of Nottingham, and from controlled environment experiments. The BAMnut model (Bannayan, 2001; Azam-Ali et al., 2001) used the original PARCH model (Bradley and Crout, 1993) and combined with GIS mapping to give yield predictions globally. Subsequently in 2000, the International Cooperation with Developing Countries Programme of the EU funded the second research project on bambara groundnut entitled “Increasing the productivity of bambara groundnut for sustainable food production in semi-arid Africa (BAMFOOD)” resulted the second crop model (Cornelissen, 2005). The BAMFOOD project model attempted to account for the differences between landraces in terms of growth, development and yield under water limited condition while the predictions were focussed to species *Vigna subterranea* in earlier model BAMnut. BAMFOOD project model was mainly focused on field experiments in Swaziland and adapted to predict growth, development and yield of the some landraces across a range of glasshouse environments.

The clear understanding in strengths and weaknesses in previous bambara groundnut models provided the research background to the present study. This aims to account for the differences in growth, development and yield of bambara groundnut landraces for major abiotic stress factors in suitable model; BAMGRO. In this thesis, the development of a new crop model (BAMGRO) for an indigenous crop bambara groundnut (*Vigna subterranea* (L) Verdc.) is presented. BAMGRO is based on the established CROPGRO model (Boote et al., 2002a) and integrates data from contrasting landraces and locations within the BAMLINK project (EU INCO-DEV, entitled “Molecular, Environmental and Nutritional Evaluation of Bambara Groundnut for food Production in Semi-Arid Africa and India). The features of previous bambara groundnut models, BAMnut (Azam-Ali et al., 2001; Bannayan, 2001) and BAMFOOD project model (Cornelissen, 2005) are considered in BAMGRO which offers a significant improvement to capture

landrace variability due to major abiotic stress factors. The model predicts the effect of drought, heat and cold stress independently and collectively on growth, development and yield of bambara groundnut landraces. In addition, BAMGRO estimates the effects of photoperiod on growth and yield. Simulation of water uptake using the soil water sub module follows the approaches of King et al., (2003).

A crop simulation model for an agronomically and nutritionally potential crop like bambara groundnut will provide the framework for scientific cooperation to rapidly integrate new knowledge and prioritise future research on an under-researched and under-utilised species. This new approach to model bambara groundnut responses to major abiotic stress factors provides a platform for easily incorporating other biotic and abiotic factors and extending the model to more landraces and ultimately varieties of the crop.

1.1 AIMS AND OBJECTIVES

The aim of this PhD research was to develop a crop model to simulate growth, development and yield of bambara groundnut landraces under variable climatic conditions considering major abiotic stresses: drought, heat and cold and photoperiod. The specific objectives of this study were:

1. Obtain experimental data on the time course of bambara groundnut landraces under different air temperatures and limiting and non-limiting soil moisture regimes
2. Develop landrace specific relations under drought, heat and cold stress.
3. Develop new functions for the rate of new leaf production, leaf expansion senescence, dry matter production, dry matter partitioning based on potential demand with priority and yield under variable climatic conditions.
4. Simulate root growth and root distribution, the water uptake by the root system and the soil water balance of the profile under variable climates.
5. Test the model predictions against the field sites in Africa and the glasshouse in Nottingham, UK.

1.2 THESIS OUTLINE

- **Chapter 2** is a review of existing literature on bambara groundnut and provides insight into the effect of environmental factors on growth, development and yield. The strength and weaknesses of two earlier bambara groundnut models BAMnut and BAMFOOD model, are described in detail.
- **Chapter 3** describes the experimental details of model data sets used for model parameterisation and validation and is referred to in the subsequent Chapters.
- **Chapter 4** is an overview of new BAMGRO model, the details of which are described in subsequent Chapters.
- **Chapter 5** discusses modelling canopy development of bambara groundnut landraces under abiotic stress. The model development with suitable parameterisation and simulation results are described in this Chapter.
- **Chapter 6** considers modelling dry matter production and yield under abiotic stress and describes the model development (with parameterisation where necessary) and model validation.
- **Chapter 7** describes the BAMGRO-soil water sub module, comprising model development with suitable parameterisation and simulation results for soil water balance.
- **Chapter 8** integrates the results from Chapter 5, 6 and 7, potential applications of result, make recommendations for future research and concludes by discuss how the research has achieved its aims and objectives.

CHAPTER 2

2. REVIEW OF LITERATURE

2.1 INTRODUCTION

Various studies have been conducted on the botany, crop physiology, biochemical properties, economics and modelling of bambara groundnut (Pasquet et al., 1999; Linnemann and Azam-Ali 1993; Bannayan, 2001; Cornelissen, 2005). This Chapter reviews the botanical features of the crop, climate and crop production in semi-arid Africa where it originated, crop physiology relevant to abiotic stress factors and previous modelling of bambara groundnut.

2.2 THE BAMBARA GROUNDNUT CROP

Bambara groundnut (*Vigna subterranea* (L.) Verdc) is an indigenous food crop that originated in the regions between the Jos Plateau in Northern Nigeria and Garu in Cameroon. The crop has been grown widely for many centuries and is successfully grown throughout sub-Saharan Africa. The variety *subterranea* is the cultivated form with wild forms belonging to variety *spontanea* (Pasquet et al., 1999).



Plate 2.1. Morphological features of bambara groundnut.

Morphologically bambara groundnut is very similar to groundnut (*Arachis hypogaea*), although the centre of groundnut diversity is in Latin America. Bambara groundnut has compound leaves made of three elliptic or lanceolate and glabrous leaflets. The leaves are on long petioles that originate from short stems just above ground level. The cultivated forms of bambara groundnut have stems with a limited creeping growth habit, which give rise to either bunchy or intermediate types (Linnemann and Azam-Ali, 1993). Flowers are borne on short racemes and are yellow or cream in colour. Pods contain one or two seeds formed either underground or aurally at ground level (Plate 2.1).

Bambara groundnut plays a significant role in cropping systems in semi arid Africa and is often intercropped with cereals, tuber crops, vegetables and other legumes. According to Linnemann and Azam-Ali, (1993), bambara groundnut is successfully intercropped with cassava as well as maize and sweet sorghum in Zambia. The importance of the crop in intercropping systems may be related to the improvement of soil fertility by better enhancement of nitrogen fixation compared to most other legumes. Therefore, bambara groundnut is considered to give a better residual soil fertility effect for the following crop than groundnut (Linnemann and Azam-Ali, 1993).

Bambara groundnut is cultivated as a human food by subsistence women farmers in semi-arid tropical region of Africa (Azam-Ali et al., 2001). It is grown for its seeds which are eaten fresh when semi ripe and as a pulse when dried and mature. The seeds are nutritious and contain high amount of carbohydrates and proteins with relatively low fat. Bambara groundnut is biochemically superior to most of the other legumes (cowpea, groundnut and pigeon pea (*Cajanus cajan*)) containing 16-25% protein (Brough and Azam-Ali, 1992; Onimawo et al., 1998). The protein contained in bambara groundnut is low in cysteine and methionine and the seed coat contains tannins and trypsin inhibitors (Brough and Azam-Ali, 1992). However, there are no harmful effects due to tannins and inhibitors in human diets or on protein availability because the seeds are cooked and dehulled before consumption.

The characteristic physiological feature of bambara groundnut is its drought tolerance. Consequently, there is an agronomic advantage of growing bambara groundnut in low rainfall areas compared to other legumes (Collinson et al., 1996). The average yield of bambara groundnut under favourable conditions ranges from 3.0 to 3.8 t ha⁻¹ (Linnemann and Azam-Ali, 1993; Collinson et al., 2000).

2.2.1 Bambara Groundnut Landraces

In the absence of established varieties, marginal and subsistence farmers in Africa grow locally adapted ‘landraces’ of bambara groundnut. A landrace is a locally adapted strain of a species selected through traditional methods and not influenced by modern breeding technologies. It is predominantly a self pollinated species, and isozyme diversity pattern suggests that wild populations are characterised by higher genetic diversity than cultivated forms, making them potential sources for bambara groundnut breeding and improvement (Basu et al., 2003).

Two landraces S19-3 (Namibia) and Uniswa Red (Swaziland) have been commonly used for various studies at Tropical Crops Research Unit, Sutton Bonington Campus, at the University of Nottingham, United Kingdom (Chapter 3, section 3.3). They have been identified as representative landraces for two extremes of climate where bambara groundnut can be grown. In addition, there are number of local landraces particular to each region. However, very little research has done to evaluate the growth and developmental performance of these local landraces.

2.3 CLIMATE AND CROP PRODUCTION

The climatic conditions in Semi-Arid Africa vary from humid equatorial regimes, through the seasonally-arid tropics, to subtropical Mediterranean climates. All these climates are variable, especially with regard to rainfall. The common landraces, Uniswa Red and S19-3 which dominate the current study are adapted to climates in Swaziland and Namibia respectively (section 2.3.1).

2.3.1 Climatic Characteristics of Uniswa Red and S19-3 Landraces

Original climate of landrace S19-3 in Namibia

The Namibian coast receives very little rain and is a complete desert with an average rainfall of only 22 mm per year. The interior is also marked by low rainfall and much of it is semi-desert. It receives some scanty but unreliable summer rain which increases eastwards and northwards with an annual average rainfall of 368 mm and average daily temperature varies over winter and summer. The hottest months are between November and February, with mean maximum temperatures ranging between 20 °C and 36 °C. Mean minimum winter temperatures range between 6 °C and 10 °C, and average winter day temperatures between 18 °C and 22 °C. Summer (October to April) mean interior temperatures range from 20 °C to 34 °C during the day. Temperatures above 40 °C are often recorded in the extreme north and south of the country (Pears and Smith, 1998). Therefore S19-3 can be hypothesised to have evolved with hot and dry weather and completes the life cycle at faster rate to minimize the risk of drought.

Original climate of landrace Uniswa Red in Swaziland

This small landlocked country lies at 27° S between South Africa and Mozambique. The winters are dry and mild with frequent rain and temperatures are rarely excessively high. In the higher, western parts of the country, the average rainfall is 1400 mm per year, with mean daily temperature of 17 °C. The country slopes eastwards until, along the Mozambique border, it becomes low-lying and almost tropical in its climate. In this part of the country, the average rainfall is 760 mm per year and the mean daily temperature ranges from 6 °C to 15 °C in winter and 19 °C - 25 °C during summer (Pearce and Smith, 1998). Uniswa Red survives well in this wet and cold climate with a longer crop cycle.

2.4 PHYSIOLOGY OF BAMBARA GROUNDNUT

The growth and development of bambara groundnut is affected by the major abiotic stress factors of moisture, heat and cold. Photoperiod plays a significant role in the reproductive phase of the plant by regulating flowering and pod formation. Details of the effects of these environmental factors are explained in sections 2.4.1, 2.4.2 and 2.4.3.

2.4.1 Effect of Moisture Stress

For bambara groundnut, growth and development can be categorized into a series of discrete stages from sowing to harvesting. The growth stages can be divided into the vegetative (pre-reproductive) phase and the reproductive phase. The vegetative phase is mainly characterised by continuous production of leaves and roots. This phase is highly susceptible to abiotic stress factors determining the extent to which the crop will capture resources over the season. Therefore any limitations imposed during the vegetative phase effect the reproductive phase.

Cell and leaf expansion

The literature on cell and leaf expansion of bambara groundnut is very limited. However the effect of soil moisture on cell division and leaf expansion of various other crops has been widely studied (Jones, 1992). Water deficit has considerable effects ranging from the cellular level up to the canopy level. The effect at cell level appears to trigger a series of responses, resulting in reduced productivity at the canopy level. According to Jones (1992), most of the cell biochemical processes, cell division and expansion are very sensitive to moisture stress. The expansion of leaf cells is regulated by the turgor pressure within the cells, and the reduction of turgor potential is directly correlated with reduction of cell extension rate (Squire, 1990; Turner, 1997).

Canopy development

The effect of soil moisture on Leaf Area Index (*LAI*) and leaf production has been studied extensively in field and controlled environments. Bambara groundnut has recorded lower *LAI*, under moisture stress conditions for different landraces (Mwale et al., 2007a; Berchie 1996; Bouteng, 2003). Controlled environmental studies for bambara groundnut have reported that leaf number decreased by up to 60% in drought treatments, causing a reduction in *LAI* (Collinson et al., 1996; Collinson et al., 1999). Mwale et al. (2007a) reported that soil moisture stress affected the canopy development of bambara groundnut by reducing both leaf number and *LAI* of the crop.

Root growth

Roots play a dominant role in crop growth by the uptake of water from the soil. The rate of root growth down the profile is closely related to water uptake from the soil especially the crop is grown on stored water. Generally, the major characteristics of drought avoidance in any root system are root front velocity (*RFV*), depth of rooting, root length density (L_v) and ratio of root:total dry matter.

According to Monteith (1986) the rate of root extension in drying soil is approximately equal to the extraction front velocity of water by a given root system. Few in-depth studies have been conducted on root growth in relation to soil moisture stress of bambara groundnut. Therefore the actual response of particular landraces is unclear. Mwale (2005) reported *RFV* of bambara groundnut between 28 and 42 DAS as 2.1 cm d⁻¹ in TCRU experiments and it declined with time. However, this was higher than the value of 1.6 cm d⁻¹ reported from Zimbabwe (Collinson et al., 1996). The related studies from other legumes showed *RFV* ranges between 2.0 and 3.0 for groundnut (Meinzer and Karnok, 1992) and 2.4 for chickpea (Thomas et al., 1995). The reduction in *RFV* is linked with phenology of the crop, particularly the change from vegetative to reproductive

phase when formation of reproductive organs have priority as per details reported for sorghum (Robertson et al., 1993a) and faba bean (Manchadi et al., 1998).

Average root length density (L_v , cm cm^{-3}) distribution of bambara groundnut landraces at 42 days after sowing (DAS) showed more roots were accumulated at the upper layer 0-50 cm (Kijoji, 2003). According to Mwale (2005), L_v of bambara groundnut is extremely low compared to the reported values of other common legumes such as groundnut (Rao et al., 1989), soybean (Turman et al., 1995).

Resource capture and conversion

The canopy size and its longevity determine the amount of radiation that can be intercepted by a crop. LAI has a dominant control over the radiation interception which depends on the average spectral properties of leaves and on their orientation in relation to spatial distribution of solar radiation (Monteith, 1996).

Many studies have been done on bambara groundnut to evaluate the impact of drought on fractional interception (f) and radiation use efficiency (ϵ_s g MJ^{-1}), revealing that there was a general reduction in f under drought and a variable response of ϵ_s . There was a large reduction of f in bambara groundnut due to drought and seasonal values ranges from 0.73 for irrigated treatment and 0.20 for drought conditions (Collinson et al., 1999). A similar study reported that drought reduced ϵ_s from 1.51 g MJ^{-1} to 1.02 g MJ^{-1} across landraces (Mwale et al., 2007b). Similarly, in cowpea, drought caused a reduction of f and ϵ_s by 50% and the values of ϵ_s ranged from 0.73-1.15 g MJ^{-1} to 0.51 g MJ^{-1} in irrigated and droughted treatments respectively (Craufurd and Wheeler, 1999).

Water use efficiency (ϵ_{water} g kg^{-1}) is the amount of dry matter produced per unit of water transpired. The response of ϵ_{water} (g kg^{-1}) varies to a greater extent for different crops. For bambara groundnut there was no consistent values of ϵ_{water} under drought. In controlled environment glasshouses at the University of Nottingham, however, reported ϵ_{water} values ranged between 2.02 and 3.0 g kg^{-1}

under irrigation and between 1.8 and 2.6 g kg⁻¹ for drought treatments (Shamudzarira, 1996). The most recent study on bambara groundnut, reported that drought reduced ϵ_{water} from 2.05 g kg⁻¹ to 1.65 g kg⁻¹ (Mwale et al., 2007b). The literature reported that for different species there was a reduction of ϵ_{water} under moisture stress while some describe no change and others have reported an increase in ϵ_{water} . For example, Pannu and Singh (1993) investigated the effect of different irrigation schedules on ϵ_{water} of mung bean and found the highest ϵ_{water} under drought. On the contrary, water stress for Kabuli chickpea (*Cicer arietinum* L.) did not affect ϵ_{water} (Anwar et al., 2003).

Dry matter production

As discussed earlier, there is a strong influence of drought stress on leaf production, radiation capture and conversion efficiency of radiation and water which controls the dry matter production of the crop. Dry matter production of bambara groundnut was highly responsive to the amount of water applied to the crop. Collinson et al., (1996), reported that total dry matter ranged from 9.3 t ha⁻¹ to 2.2 t ha⁻¹ under irrigated and drought treatments respectively. Shelling percentage was the most stable yield component for bambara groundnut and showed the least effect under drought (Mwale et al., 2007a). The pod number per plant was the most sensitive yield component being reduced by 43% due to drought and corresponding reductions in Harvest Index (*HI*) and seed weight were 16% and 15% respectively.

Leport et al. (1999), reported drought reduced the dry matter production of chickpea by 30-40%. These findings were supported by an independent study of Anwar et al. (2003) who found a reduction of total dry matter of kabuli chickpea under water stress. The effect of drought stress on dry matter production was further elaborated by a study conducted on soybean (De Costa and Shanmugathan, 2002). This study found that the vegetative growth of soybean was highly responsive to irrigation and podfilling stage was the least responsive.

2.4.2 Effect of Temperature Stress

In the absence of stress, temperature has a primary influence on developmental processes within the plant. It has been recognized that three cardinal temperatures (base, optimum and ceiling) describe the range of temperatures over which particular developmental processes take place (Linnemann and Craufurd, 1994). The base temperature (T_{base}) is the lowest at which development can occur, the optimum temperature (T_{opt}) is the temperature at which it is maximum, and ceiling (T_{high}) is the temperature after which the rate of development stops. The rate of many developmental processes is positively correlated with a linear function of temperature between T_{base} and T_{opt} , and a negative linear function of temperature between T_{opt} and T_{high} (Wheeler, et al., 2000). The role of temperature on vegetative development of bambara groundnut through processes such as leaf appearance and leaf expansion, has not been examined in detail (Collinson et al., 1997; Collinson et al., 1996). According to Massawe et al. (2003) the rate of leaf appearance was linearly related to temperature. Since the crop shows a considerable degree of phenotypic diversity in morphology, growth habit, and crop duration (Linnemann, 1993; Collinson et al., 1996; Collinson et al., 1997) it seems likely that the influence of temperature on vegetative development is not uniform among genotypes.

2.4.3 Effect of Photoperiod

Bambara groundnut is a short-day species. Flowering is set by thermal time whilst the onset of ‘podding’ (pod growth) is affected by photoperiod in both controlled environment studies (Linnemann, 1991a; Linnemann, 1991b) as well as in the field (Harris and Azam-Ali, 1993). Some bambara groundnut landraces are photoperiod-sensitive with regard to the time to flowering, and most are sensitive in relation to the onset of pod-filling (Linnemann and Craufurd, 1994). When day lengths are longer than the optimum (12 h), the crop will take longer to reach pod filling, delaying maturity. However, the exact mechanism by which day length imposes control over pod development in this species is unknown. Linnemann

(1993) has demonstrated that embryo development was independent of day length until 18 days after flowering when growth ceased under long photoperiods and pods were aborted.

2.5 SUMMARY OF PHYSIOLOGY OF BAMBARA GROUNDNUT

- Growth and development of bambara groundnut is affected by major abiotic stress factors: drought, heat and cold stress and photoperiod.
- Previous work reported that drought stress has an influence on canopy development through reduction of leaf production and leaf expansion compared to non moisture limited condition. Smaller canopies result in reduction of radiation capture and thereby lower dry matter production and yield.
- Temperature (heat and cold stress) is closely related to the growth and development of the crop and the literature cited indicates a linear relationship between rate of leaf production and thermal units accumulated. However the limited information explains the genotypic variance on the effect of heat and cold stress on growth and development.
- Bambara groundnut is a photoperiod sensitive, short day crop and experiences delay pod formation when the daylengths exceed 12 h.

2.6 CROP MODELLING

Crop simulation models are increasingly being used in agriculture to estimate production potentials, design plant ideotypes, transfer agro technologies, assist strategic and tactical decisions, forecast real time yields and establish research priorities (Uehera and Tsuji, 1993; Bannayan and Crout, 1999).

2.6.1 Definition

Crop models have been defined in different ways by many scientists. Monteith (1996) has defined a crop model as a quantitative means of predicting growth, development and yield of a crop, for given genetic coefficients and relevant environmental variables. Sinclair and Seligman, (1996) define crop modelling as “the dynamic simulation of crop growth by numerical integration of constituent processes with the aid of computers”.

However, the difference between *mechanistic* and *empirical* models can be illustrated by considering the process of model construction. In *mechanistic* crop models, the quantified process has a sound physical and physiological basis (Monteith, 1996). Whereas, *empirical* model functions are selected to fit the observed field and laboratory measurements (Monteith, 1996). Naturally this distinction is not always clear and there are often areas of overlap.

2.6.2 Examples of Models

Most crop models are a combination of calculations based on actual physiological processes and empirical relationships to give predictions for a particular crop (Boote et al., 1996). Some examples of models that have developed for various crops are shown in Table 2. 1.

Table 2. 1. Examples of common crop models.

Crop	Model	References
Maize	CERES-Maize	Jones and Kiniry, (1986)
Groundnut	PNUTGRO	Boote et al. (1989)
Soybean	SOYGRO	Wilkerson et al., (1985)
Faba bean	CROPGRO-Faba bean	Boote et al. (2002a)
Tea	CUPPA-TEA	Matthews and Stephens (1998a)
Chickpea	CHICKPGRO	Singh and Virmani (1996)
Cassava	GUMCAS	Matthews and Hunt (1994)
Wheat	WTGROWS	references
	SWHEAT	
	CERES-Wheat	
Bambara groundnut	BAMnut	Bannayan (2001)
	BAMFOOD model	Cornelissen (2005)

2.6.3 Complex versus Simple Models

The two extremes of simple and complex models do not represent actual crop modelling situations. The level of complexity depends on the objectives of the study, availability of data and time for model development and testing (Boote et al., 1996). Complex models require a lot of parameters and can lead to cumulative errors in the model (Sinclair and Seligman, 1996). The use of statistical techniques for model evaluation and sensitivity analysis of input parameters will provide pathways to minimise the number of parameters in complex models.

2.6.4 Limitations of Crop Models

The most common problem of crop modelling is their limited validity. Some models are developed in a particular environment and are not validated for the conditions in which they are applied (Monteith, 1996). Most crop models are built combining well established relationships that have been tested over a wide range of environments, and new hypothesis for the chosen environments. Under this situation it is difficult to test the model as a whole unit (Monteith, 1996).

2.6.5 Use of Crop Models

Crop models are used extensively for estimation of crop yields (Azam-Ali et al., 2001; Robertson et al., 2001), management, education, decision support system, crop genotype improvement, defining research priorities, technology transfer and predicting the effects of climate change (Tingem et al., 2008).

2.7 PREVIOUS MODELLING

The first attempt to model bambara groundnut was through the integration of appropriate crop parameters into the PARCH model (Collinson, 1996). This led to the BAMnut model (section 2.7.1) (Bannayan, 2001; Azam-Ali et al., 2001) an improvement to the original PARCH-based model. A subsequent model for bambara groundnut was BAMFOOD project model (section 2.7.2). (Cornelissen, 2005) which used landrace specific parameters under water limited conditions.

2.7.1 BAMnut Model

This model integrates knowledge about the agro-ecological requirements of bambara groundnut across a range of locations in Africa. BAMnut (Bannayan, 2001; Azam-Ali et al., 2001) was the first dynamic simulation model for bambara groundnut and provided the first predictions of its pod yield in response to environmental factors and responses to drought stress. The model was designed with physiological relations derived from glasshouse and growth room experiments at the University of Nottingham (Kocabas et al., 1999; Collinson et al., 1999; Collinson et al., 1997; Berchie, 1996) and field experiments conducted in Africa (Sesay and Yarmah, 1996; Karikari et al., 1996).

In BAMnut dry matter production and pod yield are predicted through numerical integration over a daily timestep. The main concern of the model was to evaluate growth, development and yield depending on the availability of light and water. The production was either light or water limited depending on which resource was

most limiting in any particular daily timestep. Light Limited Growth (*LLG*) was calculated from incoming solar radiation, radiation use efficiency (ϵ_s g MJ⁻¹) and the fraction of solar radiation intercepted by the canopy. Water Limited Growth (*WLG*) was calculated from potential water uptake rate based on the amount of water available in the root zone. Actual growth was taken as the minimum of the water and radiation limited growth. Pod yield was determined at crop maturity as the product of accumulated above-ground dry matter over a constant, landrace specific, harvest index (Azam-Ali et al., 2001). The model requires input of daily data of solar radiation, minimum and maximum temperatures and rainfall.

2.7.2 BAMFOOD Project Model

The model developed in BamFood project (Cornelissen, 2005) is based on the PALM model (Matthews, 2005) and developed through field experiments in Swaziland and aimed to account for the differences among landraces in relation to growth, development and yield. The model was then adapted to make predictions for different landraces under a range of glasshouse conditions. BAMFOOD project model simulates the growth and development under water limited environments taking into account the photoperiod effect on pod formation. However, it uses a simplified approach to evaluate the effect of photoperiod, ignoring landrace differences. In the model, plant water balance routines were adapted using the features of PALM model (Matthews, 2005) and two water factors: plant water factor1 (WM_1) and plant water factor 2 (WM_2) were considered for modifying dry matter production and leaf area expansion under water limited environments respectively. One of the major limitations during the development of the model was the lack of data on the water status of the soil. Neither initial water content, nor water content of the soil over the season was measured in the field. The initial water content of the soil and the water release characteristics of the soil during the simulations were therefore assumed. The model reduces growth and leaf area expansion using PALM water routines (Matthews, 2005). This agrees with literature (Mwale et al., 2007a, Mwale et al., 2007b, Collinson et al., 1999, Collinson et al., 1996). Phenology, however, is unaffected by drought.

2.8 SUMMARY OF MODELLING BAMBARA GROUNDNUT

- Crop models provide quantitative information for growth of a crop for a given set of environmental data sets and genetic coefficients.
- Well established crop models are abundant in literature for major crops in literature while very few attempts were taken for bambara groundnut.
- The modelling of bambara groundnut was initiated through integration of crop parameters in to the PARCH model and it was extended to dynamic crop model BAMnut which integrated the crop parameters under water limited and light limited conditions.
- The most recent model, BAMFOOD model simulated the growth, development and yield of bambara groundnut landraces under drought considering two plant water factors affect on dry matter production and leaf area expansion.

CHAPTER 3

3. EXPERIMENTAL DETAILS OF MODEL DATA SETS

3.1 INTRODUCTION

This Chapter describes the materials and methods of the experiments (including some not undertaken by the author) that are used to derive model data sets for the BAMGRO model. The model was mainly parameterised using data from glasshouse experiments (Tropical Crops Research Unit-TCRU) in 2006 (section 3.3.2). Additional parameters were derived from TCRU experiments prior to 2006 (section 3.5). Initially, the model was validated for 2007 and 2008 TCRU experimental data sets (sections 3.3.3 and 3.3.4) respectively. Model calibration for different photoperiod levels was done using data from growth room experiments at the University of Copenhagen, Denmark (section 3.2.1). BAMGRO was validated for field sites in Botswana and Swaziland where every site followed the same experimental protocol (section 3.4). These experiments are summarised in Table 3.1.

Table 3. 1. Summary of experiments used for model data sets.

Experiment	Location and year	Major abiotic stress	Section number
Growth room	University of Copenhagen, Denmark (2006-2008)	Photoperiod levels	0
Glasshouse (TCRU)	University of Nottingham, UK (2006)	Heat and cold	3.3.2
Glasshouse (TCRU)	University of Nottingham, UK (2007)	Heat, cold and drought	3.3.3
Glasshouse (TCRU)	University of Nottingham, UK (2008)	Heat, cold and drought	3.3.4
Field	Botswana (2006-2008)	Heat, cold drought and photoperiod	3.4.1
Field	Swaziland (2002-2003)	Drought	0
Previous	University of Nottingham, UK	Various stress	3.5

3.2 GROWTH ROOM EXPERIMENTS

3.2.1 Effect of Photoperiod

The data sets from growth room experiments were used for parameterisation of the model. An experiment at the University of Copenhagen supported the model calibration for different photoperiod levels through the EU- BAMLINK project. Two bambara groundnut landraces (Uniswa Red and S19-3) were tested for phenological development under controlled environment (C-E) conditions at five day lengths (10 h, 11 h, 12 h, 13 h and 14 h) at the University of Copenhagen, Denmark. Plants were grown in pots (20 cm diameter, 3.5L) using sphagnum moss as a growing media and temperature was 26 °C at night and 30 °C at daytime. Pots were irrigated daily with a drip irrigation system which contained full nutrient solution especially nitrogen (N) to avoid variation between genotypes in N-fixing ability. The experimental setup was split-plot with four replicates. Six plants per landrace were used as subplots to compensate for the lack of uniformity of the landraces tested. This protocol provided data from 24 plants per treatment. Through the growth cycle non-destructive growth and developmental measurements were made. (BAMLINK, annual report, 2007).

3.3 GLASSHOUSE EXPERIMENTS: TROPICAL CROPS RESEARCH UNIT

This section explains three glasshouse experiments that were conducted from 2006 to 2008. Two experiments (2006-7) were done as a part of this PhD research providing data for model parameterisation and validation respectively. Additional validation data sets were taken from a BAMLINK project experiment in 2008. There are some common features to these three experiments which are explained below (section 3.3.1).

3.3.1 Common Features

Experimental location

The three main experiments were conducted at the five glasshouses of the Tropical Crops Research Unit (TCRU) at the University of Nottingham, School of Biosciences, Sutton Bonington Campus, United Kingdom (52° 50' north, 1° 15' west; 45 m altitude). They are aligned in a North-South direction to reduce structural shading and 15 m apart to avoid mutual shading (plate 3.1).



Plate 3.1. Layout of five glasshouses in Tropical Crops Research Unit, University of Nottingham, United Kingdom.

Glasshouse structures and conditions

The TCRU glasshouse (Cambridge Glasshouse Company, UK) are of conventional aluminium and glass construction erected as part of long term research on agro-physiology of tropical crops under controlled conditions. The dimensions of each glasshouse are: 10.1 m long, 4.7 m wide, 2.3 m high at the eave and 3.5 m to the central ridge (Monteith et al., 1983). These dimensions provide a cropping area of 32 m² and a pathway of 0.2 m around the perimeter of each house. A gravelly/

stony sand subsoil was overlaid by 0.3 m of sandy loam soil is. The soil PH was monitored at the beginning of each season and remained at a mean of 6.7 ± 0.2 .

Butyl sheeting has been used to line each house by digging out the soil to a depth of 1.25 m. This prevents horizontal and vertical water seepage from and to the external environment and also separates the plots within the house. This facilitates an efficient control of water treatments within each plot. The excavated soil was replaced carefully to restore the soil profile with 0.3 m loamy “plough soil” overlying a gravel loam subsoil (bulk density of 1.41 g cm^{-3}). Four “dip wells” (two in each plot) of one meter depth have been installed to pump out excess water from the houses. Four aluminium access tubes are installed in each plot to monitor the soil water content by capacitance probes (PR2; Delta-T Device). The access tubes allow soil water content to be measured to a depth of 100 cm.

A trickle irrigation system with plastic pipes (seep hose) which can be directed to each crop row is fitted to each house. A portable building erected on the same site of the glasshouses acts as the office of the TCRU and coordinates a central control computer system used to control temperature, ventilation, humidity and CO_2 concentration in each house separately (Monteith et al., 1983).

A gas-fired heater of 18 kw capacity (Powermatic Ltd, UK) controls air temperature in each glasshouse. Two directional baffles positioned at the top of each heater injects hot air to increase the temperature and it is lowered by automatically opening roof vents which run the full length of glasshouse on each side of the central apex. Air is continuously blown through the baffles, whether the heater is on or off to ensure adequate mixing of the air. The spinning disc humidifiers (Mellor-Bromley, UK), mounted at a height of 2.4 m above ground level and adjacent to the gas heaters increases humidity of the air in each house and saturation deficits are achieved by heating and ventilation. Tube solarimeters are installed in each house above and below the canopy to record the incident, reflected and transmitted radiation by each crop stands. Readings were recorded every 30 seconds on a data logger (Campbell Scientific CR 10) and averaged for every hour (Plate 3.2).

Plant materials

The two distinct bambara groundnut landraces used in these experiments were Uniswa Red (Swaziland) and S-19-3 (Namibia). The landraces were selected to represent two crops selected in contrasting climatic conditions (hot and dry; cool and wet) experienced in Africa where bambara groundnut can be grown. Both landraces were sown at 5 cm depth at 10 cm interval in rows spaced 30 cm apart.



Plate 3.2. Glasshouse facilities and structures use to control the inside environment.

3.3.2 Experiment 1: Effect of Temperature

Treatments

During the 2006 growing season, Uniswa Red and S19-3 were grown in each of the five glasshouses. Two temperatures: 23 ± 5 °C (LT) and 33 ± 5 °C (HT) were imposed according to the following plan (Figure 3.1). Soil moisture in each house was non-limiting and irrigation was applied each week to field capacity.

The treatments (two bambara groundnuts landraces and two different temperature regimes) were allocated in a split-plot design with each treatment replicated twice and thrice at low and high temperature, respectively, due to limited number of glasshouses (Figure 3.1).

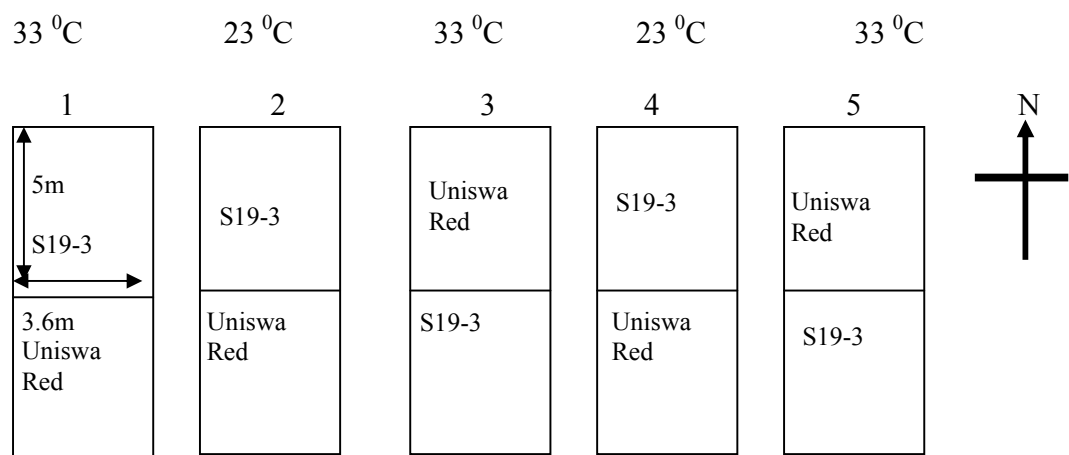


Figure 3.1. Layout of landraces and temperature treatments in five glasshouses in 2006.

Crop husbandry practices

Soil preparation and fertilizer application

Approximately 300 kg ha⁻¹ of Potassium and 100 kg ha⁻¹ of Nitrogen were applied to all plots at 57 days before sowing (DBS) and 34 days after sowing (DAS)

respectively. Soil cultivations started at 5 DBS. These included hand-cultivation and rake-harrowing to create a fine tilth seedbed.

Plant population

A total of 432 seeds per plot, sourced from 2005 TCRU experiments (irrigated bambara groundnut crop), were sown on May 11, 2006. Three seeds per each hole were sown at a depth of 5 cm, 10 cm within rows and 35 cm between rows. Thinning was done at 19 and 22 DAS, in glasshouses at high and low temperature, respectively, to the spacing of 35 cm by 20 cm, leaving a plant density of 15 plants per m² until harvest.

Day length screening

As bambara groundnut is a short-day plant, the day length was controlled to 12 h per day from 21 to 113 DAS. This was done by covering the crop stand with a black polythene screen, fitted over a metal frame above the crop, everyday between 2000 and 0800 h.

Crop protection

Crops were protected against pests by both chemical and biological methods. Red spider mites (*Tetranychus cinnabarinus*) were controlled using red spider mite predators (*Phytoseiulus persimilis*) (Syngenta Bioline Production Ltd, Essex, UK) in all glasshouses at 26 DAS then on a weekly basis from 47 to 96 DAS. Two chemicals were applied against red spider mites: Dynamec (abamectin B1) in glasshouse 5 at the rate of 0.5 ml per litre of water at 40 DAS and Torq (fenbutatin oxide) in glasshouse 1 at the rate of 0.5 g per litre of water at 81 DAS.

Irrigation

The trickle irrigation system was operated in order to irrigate each plot to field capacity once in every week from 0 to 97 DAS. The amount of water applied to each plot was estimated from potential evaporation calculations for the two temperature treatments. Thus, 33 ± 5 °C treatment plots received about 56 mm more than the 23 ± 5 °C plots over the season (Table 3.2).

Table 3. 2. Amounts of water (mm) applied to the two temperature treatments over the season in 2006.

Temperature	$23 \pm 5^{\circ}\text{C}$		$33 \pm 5^{\circ}\text{C}$		
G/house Number	2	4	1	3	5
DAS	00	10	10	10	10
	04	10	10	10	10
	07	10	10	10	10
	12	07	07	10	10
	19	07	07	10	10
	22	10	10	10	10
	25	10	10	10	10
	27	22	22	22	22
	34	25	25	25	25
	41	30	30	30	30
	48	30	30	30	30
	55	40	40	40	40
	62	40	40	40	40
	69	30	30	40	40
	76	30	30	40	40
	83	30	30	40	40
	91	20	20	30	30
	97	20	20	30	30
TOTAL	381	381	437	437	437

Experimental Measurements

Developmental measurements

Emerged seedlings were counted every morning between 5 and 16 DAS in the central five rows of each plot. Each emerged seedling was tagged with a white peg on which the date of emergence was recorded. In this study, a seedling was considered to have emerged when its first pair of leaves had broken from the soil. The recorded values were converted to percentage, based on the number of seeds sown in the central five rows. After 16 DAS, 10 plants were randomly tagged in each plot and used for counting leaves, flowers and pods twice per week, starting at 35 DAS until 127 DAS.

Growth analysis

A sample of 10 plants from each plot was selected randomly every 2 weeks and for eight sequential growth analyses from 33 DAS to 131 DAS. The number of

leaves and pods on each plant were recorded after each plant was separated into leaves, pods and stems. The green leaf area of each plant was measured using a leaf area meter-model LI-3100 (LI-COR, inc. Lincoln, Nebraska, USA) and Leaf Area Index (*LAI*) was determined at each growth analysis. The leaves, stems and pods were dried separately for 48 h in an oven maintained at 80 °C and weighed. The mean of 10 plants for each variable was then calculated and recorded as the value for a particular replicate.

Yield measurements

The final harvest sample was taken from the central 3.6 m² of each plot (approximately 40 plants). Plants in this area were harvested and separated into pods and leaves before drying them for 48 h at 80 °C. The yield potential at two temperatures was calculated using the pod weight in this central harvesting area. The harvest index (*HI*) was calculated as the fraction of pod dry weight to total plant weight at harvest.

Radiation measurements

For all the TCRU-glasshouse experiments in Nottingham, UK, incoming (S_i) and transmitted solar radiation (S_t) through the canopies were measured between 20 DAS sowing until maturity using tube solarimeters installed in each house above the canopy and below the canopy. All the measurements of solar radiation were taken daily between 0800 h and 2000 h at 10-minute intervals using Campbell Scientific CR 10 data loggers (Campbell Scientific Ltd., UK) and integrated to give hourly and daily totals and are used to calculate the radiation use efficiency (ϵ_s) for each landrace.

In addition, daily minimum and maximum temperature, saturation deficit and irrigation amounts were recorded for each glasshouse throughout crop cycle

3.3.3 Experiment 2: Effect of Temperature on Crop Experiencing Late Season Drought

Treatments

Over the summer months of 2007 (April 2007 to September 2007), two bambara groundnut landraces (Uniswa Red and S19-3) were grown in all five glasshouses with each house having a Uniswa Red and S19-3 plot under controlled temperature conditions. Two temperatures, $23 \pm 5^{\circ}\text{C}$ (LT) and $33 \pm 5^{\circ}\text{C}$ (HT) were imposed according to plan shown in Figure 3.2. Soil moisture in each house was non-limiting with weekly irrigation to field capacity up to 77 days after sowing and no irrigation after this point (Table 3. 2).

As in the 2006 experiment, the treatments were allocated according to split plot design that combined two bambara groundnuts landraces with the two different temperature treatments. Each treatment was replicated twice and thrice at low and high temperature respectively, due to the limited number of glasshouses.

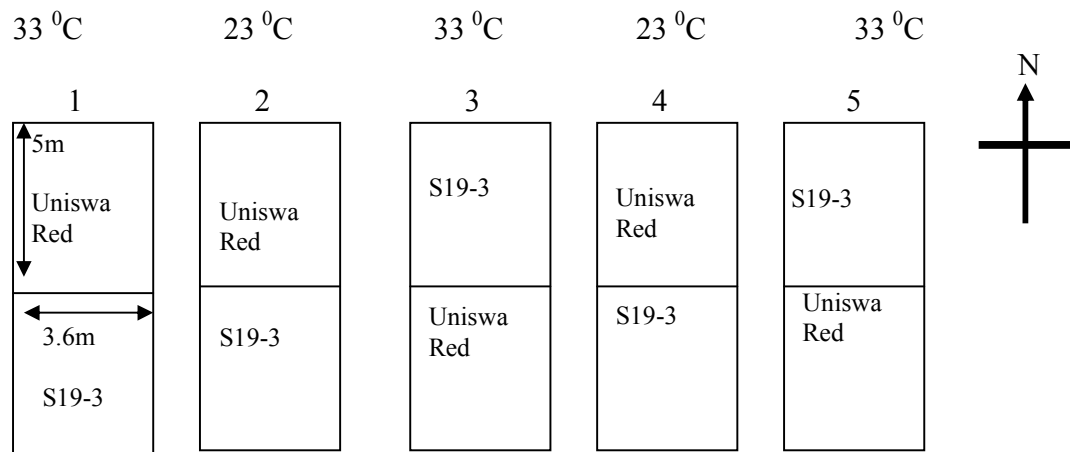


Figure 3.2. Layout of landraces and temperature treatments in five glasshouses in 2007.

Crop husbandry practices

Soil preparation, fertilizer application and day length screening were similar as described for experiment 1 (3.3.2). Seed sowing and maintenance of plant population by thinning followed the experimental protocol in 2006 (3.3.2).

Irrigation

In each glasshouse, all the plots were irrigated to field capacity once a week from 0 to 77 DAS using pipes for trickle irrigation. Each plot received an amount of water estimated from potential evaporation calculations for the two temperature treatments.

Experimental Measurements

Growth, developmental and yield measurements

Developmental, growth and yield measurements were undertaken broadly according to the experimental protocol of experiment 1 (section 3.3.2). The main difference was 9 growth analysis were completed over 158 days.

At final harvesting, pod weight for each individual plant was recorded to estimate the intra-landrace variability. The frequency distribution of pod weight can be used to eliminate the outliers from the seed source for experiment 3 (2008) and field experiments in Botswana.

Related BAMLINK Projects

Parallel measurements were performed by a PhD student (Ibraheem Al-shareef) with TCRU 2007 experiment as explained below.

Soil moisture content

Soil moisture content in the soil profile was monitored in all plots using a PR2 probe. Measurements were taken weekly starting from 55 DAS. Unfortunately the PR2 broke down after 119 DAS so the measurements are unavailable between 119 and 168 DAS. The PR2 probe measures the soil moisture at 10 cm, 20 cm, 30 cm, 40 cm, 60 cm, and 100 cm. Each plot has four access tubes, the average of the access tubes readings represent the mean amount of water in the soil for each plot.

Experimental results

The statistical analysis of growth measurements from TCRU-2006 and TCRU-2007 experiments are summarised in Table 3.3. The TCRU-2006 and TCRU-2007 experiments consisted of 8 and 9 sequential growth analysis respectively. The statistical results from 5 out of 8/9 approximately similar harvesting events representing early season, mid season and late season from each experiment (TCRU-2006: 33 DAS, 47 DAS, 75, 117 DAS, 131 DAS; TCRU-2007: 33 DAS, 47 DAS, 75 DAS, 103 DAS, 145 DAS) are shown in Table 3.3. The results were analysed as a split-plot analysis of variance with glasshouses as the main plots with temperature as the main plot factor and landraces as the subplot factor. The actual design is given earlier. Since south plot in glasshouse 1 was an extreme outlier during the growing season 2007, the results were analysed removing this plot (HT treatment) which reduced the degrees of freedom from 3 in TCRU-2006 to 2 in TCRU-2007 (Table 3.3). According to the experimental evidences in 2006, *LAI* was significantly lower ($p < 0.05$) in LT (23 ± 5 °C) compared to HT (33 ± 5 °C) during the late season. There was a significant difference ($p = 0.04$) between two tested landraces at final harvesting (131 DAS) that resulted higher *LAI* in Uniswa Red compared to S19-3. However the landrace was not significant ($p > 0.05$) before 131 DAS. Reported *TDM* was significantly ($p < 0.05$) higher in HT for both landraces compared to LT. In contrast, LT reported significantly higher ($p < 0.05$) pod yield during late season compared to HT; the significant interaction ($p=0.020$) indicating that the size of this effect differed between landraces (Table 3.3). TCRU-2007 experiment with late drought (77 DAS) showed different growth performances (Table 3.3.) compared to irrigated treatments in TCRU-2006. *LAI*, showed significantly ($p < 0.05$) lower results at 103 DAS to final harvesting (145 DAS) under LT compared to HT. In addition, S19-3 reported significantly higher ($p > 0.05$) *LAI* compared to Uniswa Red at early (33 DAS) and mid seasons (75 DAS and 103 DAS). The yield performance under LT was significantly ($p < 0.05$) higher compared to HT during mid season (75 DAS and 103 DAS). Under the soil moisture limited condition, there was a significant interaction for *LAI* on DAS 103 ($p=0.007$) indicating the two landraces were responding differently to temperature.

Table 3.3. Summary of analysis of variance (ANOVA) results from growth analysis in TCRU experiments 2006 and 2007.

Year	DAS	Variable	UN 23	S19 23	UN 33	S19 33	Temperature p	Landrace p	Temperature .Landrace	sed1	df1	sed2	df2	sed3	df3
2006	33	LAI	0.107	0.114	0.188	0.240	NS (p=0.30)	NS (p=0.11)	NS (p=0.25)	0.083	3.22	0.024	3	0.019	3
2006	47	LAI	0.361	0.394	0.729	1.016	NS (p=0.19)	NS (p=0.154)	NS (p=0.272)	0.267	2.44	0.130	2	0.106	2
2006	75	LAI	1.56	1.70	2.86	3.02	NS (p=0.107)	NS (p=0.791)	NS (p=0.988)	0.767	3.94	0.811	2	0.662	2
2006	117	LAI	2.11	1.80	5.14	4.05	S* (p=0.015)	NS (p=0.197)	NS (p=0.477)	0.705	5.96	0.742	3	0.606	3
2006	131	LAI	2.03	1.75	4.91	4.02	S* (p=0.02)	S*(p=0.04)	NS (p=0.22)	0.599	3.73	0.308	3	0.251	3
2006	33	Yield g m ⁻²	0	0	0	0									
2006	47	Yield g m ⁻²	0	0	0	0									
2006	75	Yield g m ⁻²	1.07	4.79	0.14	1.43	NS (p=0.177)	S (p=0.026)	NS (p=0.086)	1.22	2.52	0.59	2	0.481	2
2006	117	Yield g m ⁻²	126.8	156.3	44.6	101.4	S* (p=0.027)	NS (p=0.06)	NS (p=0.46)	23.58	6	25.46	3	20.79	3
2006	131	Yield g m ⁻²	209.8	162.7	55.0	149.9	S* (p=0.042)	NS (p=0.089)	S* (p=0.020)	29.07	5.10	24.24	3	19.79	3
2006	33	TDM g m ⁻²	7.94	8.87	17.06	17.97	NS (p=0.13)	NS (p=0.64)	NS (p=0.99)	4.73	3.96	2.76	3	2.25	3
2006	47	TDM g m ⁻²	30.7	29.4	56.1	83.6	NS (p=0.213)	NS (p=0.299)	NS (p=0.344)	27.35	3.06	18.25	2	14.90	2
2006	75	TDM g m ⁻²	177.1	169.4	340.0	324.2	S* (p=0.019)	NS (p=0.642)	NS (p=0.880)	35.4	3.98	36.65	2	29.93	2
2006	117	TDM g m ⁻²	413	409	553	674	S* (p=0.07)	NS (p=0.34)	NS (p=0.39)	95.6	5.91	97.9	3	79.9	3
2006	131	TDM g m ⁻²	466.0	392.0	617.0	635.0	S* (p=0.01)	NS (p=0.47)	NS (p=0.15)	36.7	5.83	36.7	3	30.0	3
2007	33	LAI	0.030	0.052	0.058	0.090	S* (p=0.01)	S* (p=0.02)	NS (p=0.39)	0.007	4.98	0.007	2	0.006	2
2007	47	LAI	0.162	0.130	0.251	0.488	NS (p=0.063)	NS (p=0.109)	NS (p=0.105)	0.09	4.69	0.073	2	0.060	2
2007	75	LAI	0.22	0.360	0.498	0.706	NS (p=0.126)	S* (p=0.008)	NS (p=0.171)	0.148	3.08	0.025	2	0.021	2
2007	103	LAI	1.49	0.93	4.20	5.38	S*(p=0.01)	S*(p=0.02)	S* (p=0.007)	0.610	3.08	0.110	2	0.090	2
2007	145	LAI	1.41	0.43	3.26	3.06	S*(p=0.026)	NS(p=0.454)	NS (p=0.563)	0.785	4.72	0.876	2	0.715	2
2007	33	Yield g m ⁻²	0	0	0	0									
2007	47	Yield g m ⁻²	0	0	0	0									
2007	103	Yield g m ⁻²	60.6	87.6	6.6	52.1	S* (p=0.040)	NS (p=0.152)	NS (p=0.644)	21.46	4.01	26.67	2	21.78	2
2007	145	Yield g m ⁻²	232	159	81	322	NS (p=0.943)	NS (p=0.155)	NS (p=0.097)	92.6	4.89	81.7	2	66.7	2
2007	33	TDM g m ⁻²	2.26	3.48	3.83	5.94	S* (p=0.017)	S* (p=0.018)	NS (p=0.21)	0.483	4.59	0.376	2	0.307	2
2007	47	TDM g m ⁻²	10.3	8.6	15.8	32.6	S* (p=0.043)	NS (p=0.074)	NS (p=0.08)	5.17	4.75	4.30	2	3.51	2
2007	75	TDM g m ⁻²	69.2	156.8	115.0	154.3	NS (p=0.54)	S* (p=0.032)	NS (p=0.159)	33.93	3.67	17.04	2	13.91	2
2007	103	TDM g m ⁻²	192	170	312	414	S* (p=0.040)	NS (p=0.177)	NS (p=0.140)	58.2	4.29	40.3	2	32.9	2
2007	145	TDM g m ⁻²	405	241	768	635.0	NS (p=0.272)	NS (p=0.331)	NS (p=0.105)	244.4	3.62	118	2	96.4	2

Sed1= standard error of difference for comparing means on different temperatures
Sed2= standard error of difference for comparing landraces at 23 degrees C
Sed3 =standard error of difference for comparing landrace means at 33 degrees C

df1= degrees of freedom for comparing means on different temperatures.
df2 = degrees of freedom for comparing landraces at 23 degrees C
df3 = degrees of freedom for comparing landraces at 33 degrees C

3.3.4 Experiment 3: Effect of Temperature and on Crop Experiencing Early Season Drought

Over the summer months of 2008 (April to September) the same experimental protocol of 2007 was repeated. Two temperatures $23 \pm 5^{\circ}\text{C}$ (LT) and $33 \pm 5^{\circ}\text{C}$ (HT) were imposed to the five glasshouses according to Figure 3.3. Soil moisture in each house was non-limiting with weekly irrigation to field capacity up to 33 DAS and no irrigation after this point.

The major experimental measurements: growth, development, yield and soil moisture were performed according to the experimental protocols of 2006 and 2007 by two PhD students (Ibraheem Al-shareef, Stanley Noah)

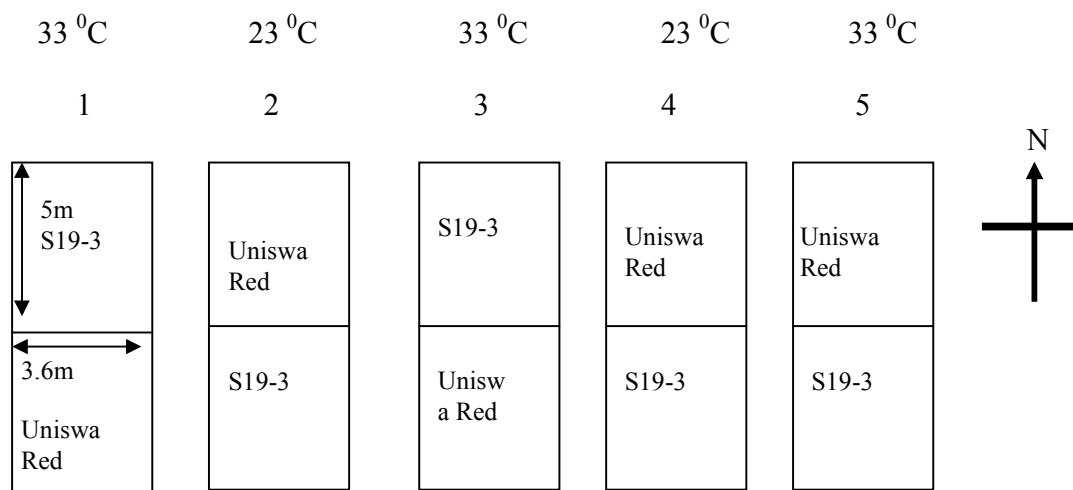


Figure 3.3. Layout of landraces and temperature treatments in five glasshouses in 2008.

3.4 FIELD EXPERIMENTS

The EU project BAMLINK includes institutions in both Africa and India as field partners. Each partner institute is mainly responsible for one abiotic factor and combined it with other abiotic stress factors when experimental facilities available. In addition the effect of the day length on growth and yield was evaluated by adjusting the sowing dates. However, some experimental failures in Tanzania and India resulted in loss of data for model validation. Therefore, the BAMGRO model was only validated for field data in Botswana and data from previous studies (Cornelissen, 2005) in Swaziland (section 3.4.1 and section 0).

3.4.1 Experiment 1: Botswana College of Agriculture, Botswana

The determination of tolerance to heat stress, drought stress and photoperiodic control of pod filling under field conditions, using the cropping calendar was performed in field sites of the experimental farm, Notwane, Botswana College of Agriculture. Four of the five agreed sowing dates, December 21, January 4, January 18 and February 1 were used in the 2006/2007 and 2007/2008 growing seasons, in order to provide a range of field environmental conditions. Out of four landraces grown in Botswana during 2006-2007 cropping season, three were selected for the validation of BAMGRO (Uniswa Red, DipC and OM1). The experiment was conducted using a single split plot design with the four sowing dates in main plots and the landraces in the sub plots, replicated four times.

In Botswana field experiments, sequential leaf counting and leaf area measurements were conducted at regular two-week intervals during the growing period. The leaf area per plant was estimated from length and width (Cornelissen et. al, 2002). In addition, harvest and final harvest data were recorded for the calculation of pod weight, yield, shelling % and harvest index. Neutron probe was used weekly to determine the soil moisture content in the profile of Botswana field experiments (2007-2008).

3.4.2 Experiment 2: Swaziland

As described by Cornelissen (2005), from December 2002 to May 2003 a set of Swaziland and Botswana landraces were grown in field sites in Swaziland (Malkerns and Luve), three of which (Uniswa Red, DipC and OM1) were selected for the validation of BAMGRO as they were common to the landraces grown in Botswana over 2006/2007 season. During the experimental period the Malkerns site reported well distributed rainfall thus suggesting no water limitation while the crop experienced a severe drought stress in the Luve field site. Both sites in Swaziland, leaf counts were carried out twice a week for the duration of the experiment on 10 pre selected plants which were tagged after emergence. Similar to the Botswana experiment the leaf area per plant was estimated from length and width (Cornelissen et. al, 2002).

3.5 PREVIOUS TCRU EXPERIMENTS

The thesis describing previous Tropical Crop Research Unit experiments on bambara groundnut were reviewed and an information matrix was produced (Table 3.4). There are approximately 20 theses on this subject (MSc mostly). More than 95% of the experiments were focused on identification of the water relations of the crop. Comparisons of different landraces and different species with bambara groundnut under two moisture regimes were done extensively. These experiments revealed that bambara groundnut, as a species has a higher potential to withstand drought while some landraces perform better under soil moisture stress conditions. Very few experiments were focused on genetic aspects of the crop.

Table 3. 4. Summary of thesis produced from TCRU experiments on bambara groundnut (*Vigna subterranea* (L). Verdc.)

Name of the Student Year Degree	Title	Major parameters measures and significant results	
Dalitso Zula 1989 MSc	Germination and establishment of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) and ground nut (<i>Arachis hypogaea</i>) in response to temperature, moisture, sowing depth and seed size.	Germination: Narrow temperature regime for germination (26-36 °C) Soil moisture : Negative response on germination Plant water relations: Ψ_{H_2O} is significant, 0 to -1.0 Mpa-50% germination	
N.G. Nuer 1989 MSc	Light interception and dry matter production of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) and ground nut (<i>Arachis hypogaea</i>) under irrigated and droughted conditions.	Radiation: Irrigated $f=0.90$ $f_g = .95$ intercepted radiation=0.95 $\epsilon_s = 0.87$ RWC- 0.70 $k= 0.55$	Droughted $f= 0.80$ $f_g = 0.80$ intercepted radiation=0.75
Anne Wanjiru and Muriki 1990 MSc	Plant water relations of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) and ground nut (<i>Arachis hypogaea</i>).	Plant water relations: Ψ_l is -0.5 MPa, -0.6 MPa (86DAS), -1.8 MPa (114DAS), Ψ_π is less fluctuation, Ψ_p is decline after 114DAS	
E.J.Brown 1991 MSc	Crop water use and root systems of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) and Sorghum (<i>Sorghum bicolor</i> (L.) Moench).	Soil moisture: Surface evaporation until 69 DAS is not significant Plant water relations: Irrigated Ψ_l lowest -1.2MPa 2.0MPaRWC- 92-96% Ψ_π -0.007 MPa Average transpiration rate at 41-90DAS is 0.6mm d^{-1} Growth analysis: Maximum root weight is 98 g m $^{-2}$	
		Droughted Ψ_l droughted declined rate 0.097 MPa d^{-1} and lowest - RWC – 90-96% Ψ_π – 0.08 MPa	

		<p>Root/total dry weight ratio is 0.07 to 0.18</p> <p>Root depth at 20 DAS is 0.5 m and at 48DAS 0.30 to 0.57</p> <p>Root length at 20DAS not significant and at 48DAS significant</p> <p>Root length density (L_v) at 48DAS higher than at 20 DAS, Top 0.30m not significant and 0.50-0.80m decline in</p>
1992	Germination and emergence of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) in relation to temperature and sowing depth	<p>Germination</p> <p>Between 6 °C – 9 °C no germination in two landraces</p> <p>$T_{(0.5)}$ – reduce with increase in temperature</p> <p>R_g(rate) is genotypic significant</p> <p>Emergence</p> <p>Time to 50% emergence significant</p>
H.E.M.Temu 1994 MSc	The effect of seed size on emergence growth and development of two landraces of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.)	<p>Soil moisture:</p> <p>Significance was due to landrace effect but not the seed size</p> <p>Radiation:</p> <p>Significance was due to landrace effect but not the seed size</p> <p>Growth analysis:</p> <p>Significance was due to landrace effect but not the seed size</p>
Joseph N.K. Bernchie 1996	Light use and dry matter production of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) landraces in relation to soil moisture stress	<p>Seedling emergence:</p> <p>Dod R > Dip C > Lun T</p> <p>Radiation:</p> <p>Fractional interception is Irrigated > droughted</p> <p>Conversion efficiency is Irrigated > droughted</p> <p>Leaf extinction co-efficient k is 0.60</p> <p>Leaf reflectivity is Irrigated < droughted</p> <p>Growth analysis:</p> <p>Leaf number is Irrigated > droughted</p> <p>Leaf area Irrigated > droughted</p> <p>LAI is Irrigated > droughted</p> <p>Leaf dry weight is Irrigated > droughted</p> <p>Stem dry weight is Irrigated > droughted</p> <p>Flower number is Irrigated > droughted</p> <p>Mean flower number highest in Dod R</p> <p>Number of pegs with out pods is Dod R > Dip C > Lun T</p>

		Total dry weight is Irrigated>droughted
Z.Shamudzarira	Water use and dry matter production in Sorghum and Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.)	Soil moisture: Mean evaporation is 1.2 mmd ⁻¹ and cumulative evaporation is 67 mm d ⁻¹ Plant water relations: Transpiration rate is not significant and soil water content declined rapidly in soil layers closest to surface. Growth analysis: Shoot growth is not significant among landraces but irrigated is significantly higher Root dry matter is significantly lower in droughted Pod yield is significantly higher in irrigated and not significant in landraces.
1996 MSc		
Daniel W. M. Wanyongo-Chintonya	Seed priming effect on emergence and early growth of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) and ground nut	Germination: Germination is 77%, priming time is significant at 95%-oh and 50%- 48 h Emergence: Priming time is not significant but interaction of genotype x priming time is significant Growth analysis: Leaf Number for interaction priming time x genotype is not significant Leaf Area is significant among genotypes and interaction of priming time x genotype is not significant Total Dry matter for interaction priming time x genotype is not significant
1997 MSc		
Gokulakannan	Phonological and genetic variation in two landraces of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.)	Emergence : Dod R-91%, Lun T- 86% Growth analysis : Leaf appearance at 67 DAS is significant (LunT> Dod R) Leaf number is LunT< Dod R Flower appearance is not significant LunT< Dod R Number of pegs is LunT> Dod R Molecular markers is not significant
1999 MSc		

Madira Dolers Edesco-Moreno 2000	Variability in the growth and development of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) landraces.	Germination and emergence: Emergence is significant Dod R > Lun T (Experiment 1) Emergence is significant Dod R, Uniswa Red > Dip C>Lun T > Namb B (Experiment 2) Growth analysis : Leaf no. per plant is not significant, flower number is significant, LA per plant is significant at 54 DAS, plant height is significant at 54 DAS, dry weight is significant (Experiment 1) Leaf no. per plant is significant, flower number is not significant, LA per plant is significant at 19 DAS, <i>LAI</i> is significant, leaf dry weight is significant at 54 DAS, total dry weight is significant (Experiment 2)
Jean Charles Deswarte 2001 MSc	Variations in the photosynthetic activity within and between landraces of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.).	Radiation: Light response curve shows a large variation. This is not significant in experiment 2 Soils moisture: Moisture level is significant Plant water relations: Transpiration is significant among landraces, stomatal conductance significant, leaf greenness is significant Stomatal density is significant Growth analysis: Leaf greenness is not significant, leaf number is significant
Mawe Bacchi Gonapa 2002	Light interception and conversion in Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) landraces in response to soil moisture.	Radiation: Diurnal fractional light interception is normal, droughted Dip C higher transmission, K is irrigated = 0.2 ($r^2=0.52$) and droughted = 0.2 ($r^2 = 0.75$) Growth analysis: <i>LAI</i> shows a steep increase in S19-3, dry weight is Droughted- S19-3 highest, Irrigated – Dip C highest
Abukakakri A. Kijoji 2003	Response of 3 Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) landraces to soil moisture stress.	Soil moisture: Surface evaporation is significant, Irrigated S19-3>Dip C Plant water relations: Stomatal conductance varied among different days, WUE irrigated>droughted Growth analysis: Crop development, leaf number is significant, shoot dry weight is significant, root:

		total dry weight is not significant among landraces, <i>RFV</i> and <i>L_v</i> are not significant (Experiment 1) Shoot dry weight, root dry matter are significant, root length density is not significant
Charles Osei Bouteng 2003 MSc	Photosynthesis of 3 Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) landraces in response to soil moisture stress	Emergence: Uniswa Red, Dip C > S19-3, crop establishment is significant Uniswa Red, Dip C > S19-3 Radiation: Fractional interception is not significant, K values are Irrigated =0.51 (r ² =0.92), Droughted= 0.45 (r ² =0.74) Growth analysis: Leaf greenness is not significant, <i>LAI</i> is significant, total dry matter increase with time, flowering is not significant
H.J.G.K.De Silva 2004 MSc	Phenotypic and genetic diversity in Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) landraces	Growth analysis: Leaf number is significant, <i>LAI</i> is significant, highest Namb B irrigated and lowest Uniswa Red droughted Total dry weight irrigated>droughted Genetics: Genotypic variation to moisture level is significant, PCR inconsistent
Justus Mtendere Martin Chintu 2004	Influence of inoculation on growth, nodulation and nitrogen fixation in 3 Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) landraces under irrigated and drought conditions.	Growth analysis: <i>LA</i> and number are significant irrigated>droughted, landraces is not significant, root dry matter is not significant Root front velocity for the growth period is significant, root length density for soil depth, harvest dates are significant, nodulation is significant, flower number is significant, nitrogen analysis is significant
M. Handa Kondjashili 2005	The effects of soil moisture on water relations and development of Bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.) and Cowpea (<i>Vigna unguiculata</i> L. WALP)	Germination : Germination is significant Cowpea>BGN-Z1>S19-3 Plant water relations: Stomatal density is significant, <i>RFV</i> , <i>L_v</i> , <i>RWC</i> , <i>WUE</i> are significant Growth analysis: Leaf Production is significant irrigated>droughted, Leaf area accumulation is significant irrigated>droughted Root:total is significant as Bambara>cowpea

S. S. Mwale	Growth of bambara groundnut in response to soil water	Germination and emergence: Landraces significant
2005		Growth analysis: Leaf number, leaf area, leaf weight, pod weight and stem weights are significant among landraces
PhD		Genetics: Genetic linkage mapping
Shravani Basu	Modelling variation in the physiology of bambara groundnut (<i>Vigna subterranea</i> (L.) Verdc.)	Modelling: Crop model developed and validated for growth, development and yield for 10 bambara groundnut landraces. Soil moisture levels are considered in relation to Leaf area expansion and dry matter production
2005		
PhD		
Rutger L.E.J. Cornelissen		
2005		
PhD		

CHAPTER 4

4. OVERVIEW OF BAMGRO MODEL

4.1 INTRODUCTION

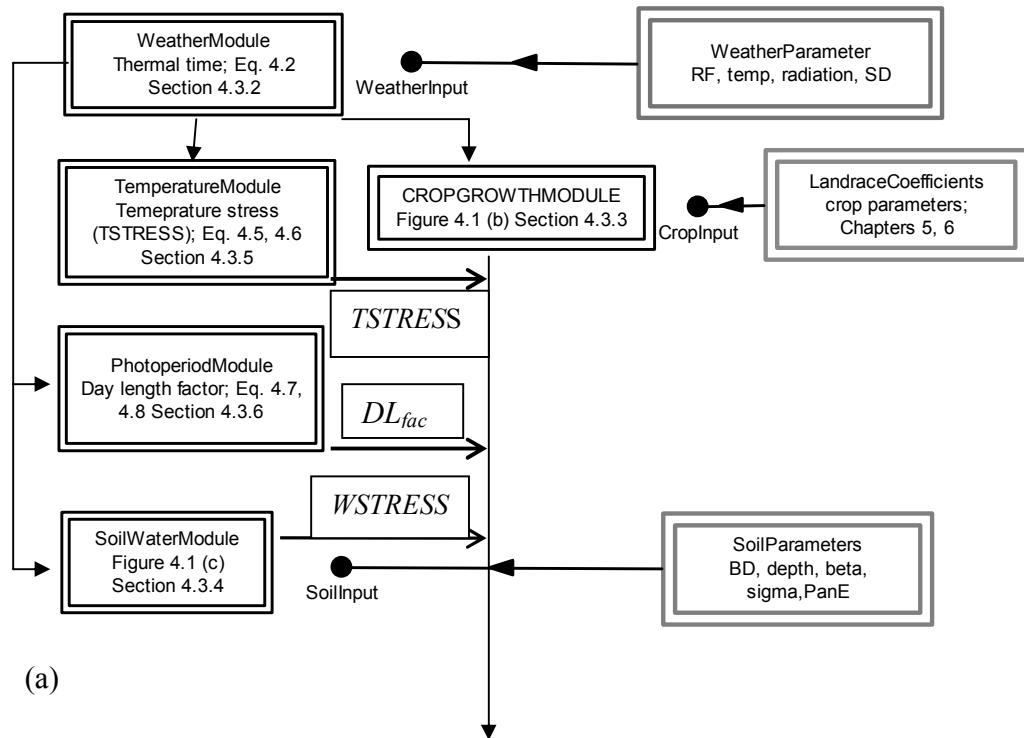
The agricultural systems in semi-arid regions of sub-Saharan Africa are normally characterised by extreme climatic conditions. Some of the most resilient crop species such as sorghum (*Sorghum bicolor*. L. Moench), pearl millet (*Pennisetum Americanum*) and cowpea (*Vigna unguiculata*). have originated from this region. Globalization challenges the existence of these indigenous crops with less resilient, but more popular crops like maize (*Zea mays*) and bean (*Vicia faba*), which are higher yielding under favourable climates. In addition, the improved breeding programmes of major crops have widened the gap between the cosmopolitan and traditional crops. Bambara groundnut (*Vigna subterranea* (L.) Verdc) is one such indigenous legume with significance as a source of protein in sub-Saharan Africa. Although there are many growth simulation models for a range of major crops, there have been few attempts to model underutilised species for which factors controlling growth and development are not well understood. A crop simulation model for an agronomically and nutritionally variable crop like bambara groundnut will provide the framework for scientific cooperation to rapidly integrate new knowledge and prioritise future research on an under-researched and underutilised species. This new approach to model bambara groundnut responses to major abiotic stress factors provides a platform for easily incorporating other biotic and abiotic factors and extending the model to more landraces and ultimately varieties of the crop. These modelling approaches linked with integrated research have useful lessons for the modelling of other underutilised crops and their potential for future agricultural systems.

In this Chapter, an overview of BAMGRO is presented; details of model development with parameterisation results are described in subsequent Chapters (Chapter 5, 6 and 7). BAMGRO is based on the established CROPGRO model (Boote et al., 2002a) and the features of previous bambara groundnut models, BAMnut (Azam-Ali et al., 2001; Bannayan, 2001) and BAMFOOD project (Cornelissen, 2005) are considered. An overview of the model structure is given in section 4.2. The summary of model components is explained in section 4.3. The details of model development, with reference to experimental results where appropriate are presented in Chapters 5, 6 and 7. The model comprises five modules for: weather (section 4.3.2), crop growth (section 4.3.3), soil water (section 4.3.4), temperature (section 4.3.5) and photoperiod (section 4.3.6). The modelling software (section 4.5) and the efficiency criteria used for the statistical evaluation of model simulations (section 4.6) are outlined as common features to Chapters 5, 6 and 7.

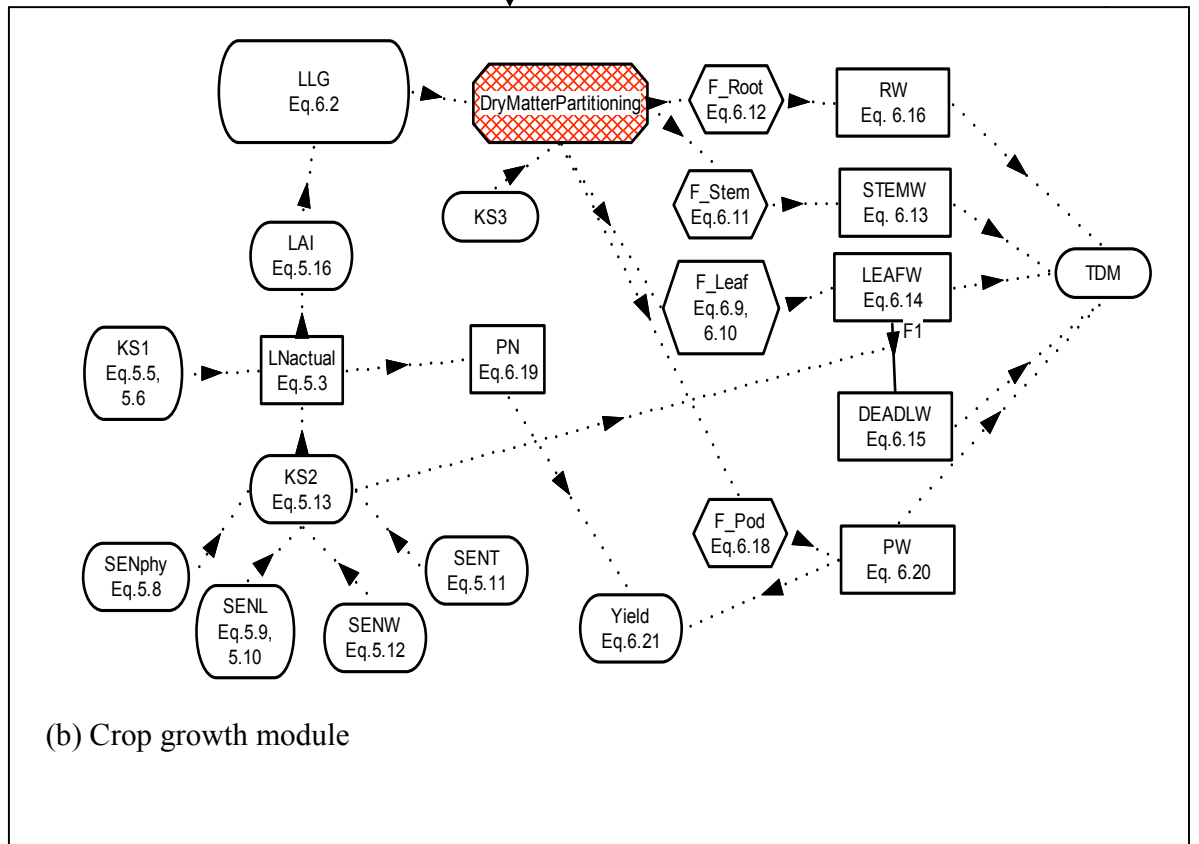
4.2 MODEL STRUCTURE AND OVERVIEW

BAMGRO consists of different sub-modules that deal specifically with weather, crop growth, soil water, temperature and photoperiod. Figure 4.1(a) shows the interactions of the main components within the model. The weather module calculates the thermal time for the developmental processes of the crop using weather data and cardinal temperatures. The crop growth module simulates canopy development (*LAI*), dry matter production (*LLG*) by means of radiation interception and yield through the partitioning coefficient (Figure 4.1(b)). The soil water sub module calculates root growth, root water uptake, water limited growth (*WLG*) and soil water balance: as inputs through rainfall and irrigation and various means of water losses through the system (Figure 4.1(c)). The temperature module calculates the temperature stress index and the photoperiod module estimates the day length factor considering the available day length and critical photoperiod 12 h.

BAMGRO is a process-oriented model that simulates a crop carbon balance and a soil water balance. The carbon balance includes daily inputs from photosynthesis and conversion of carbon into crop tissues, and losses due to abscised parts. The simulation of growth includes leaf addition, senescence, leaf area expansion, pod addition and pod filling. The main time step in BAMGRO is 1 day, but thermal time is calculated hourly and integrates over the time course of day. The model uses a daily input of weather data, and is designed to simulate canopy development, crop biomass (growth), dry matter partitioning within the crop, yield and soil water uptake. The parameters and relationships needed to build the functions in the model are derived from various field and controlled environmental experiments.



(a)



(b) Crop growth module

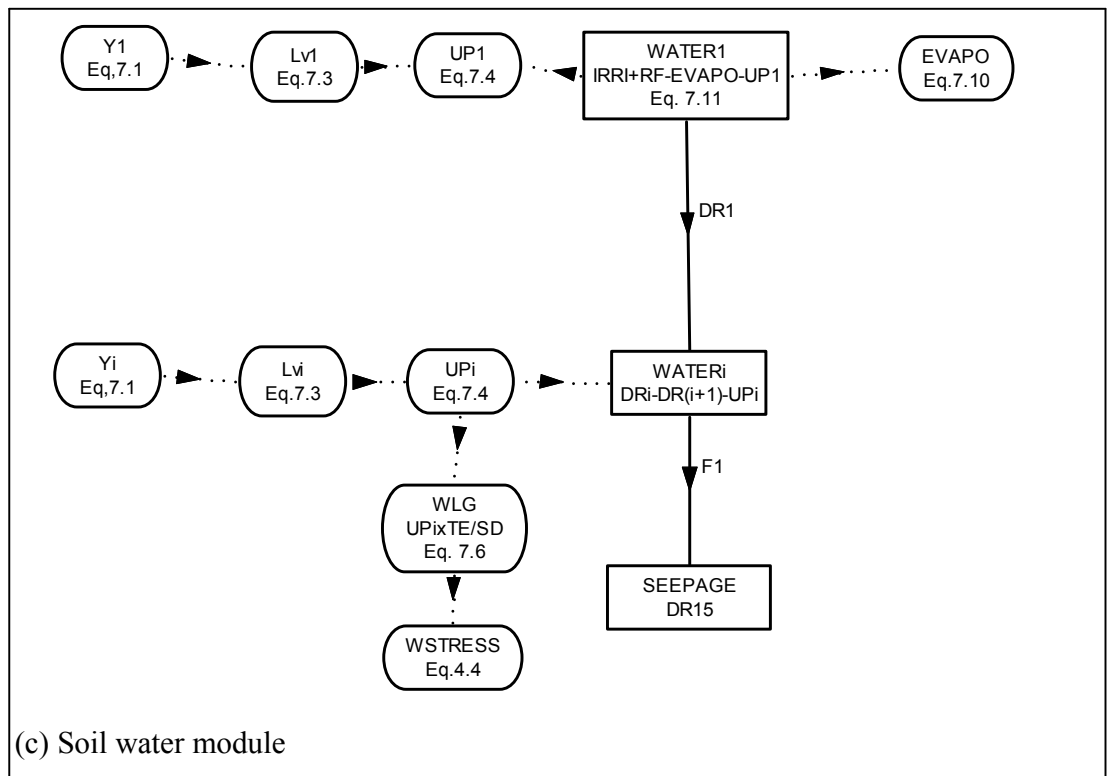
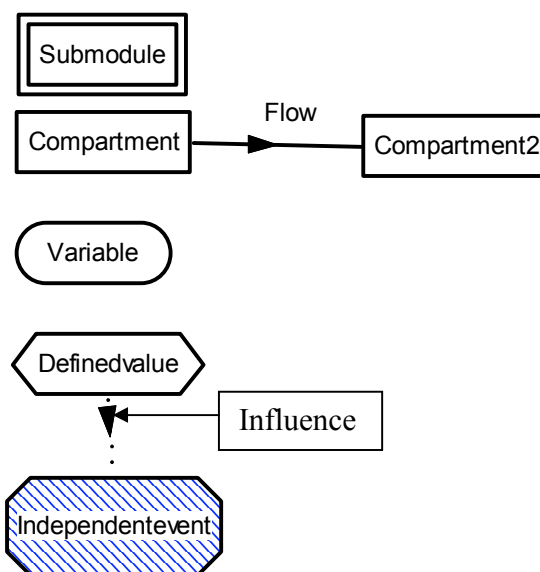


Figure 4.1. Schematic overview of data flow through the sub-modules in BAMGRO model: (a) interactions of sub-modules and input files (b) detailed diagrammatic representation of crop growth module (c) detailed diagrammatic representation of soil water module.

Key symbols in Figure 4.1 and their definitions in Model Maker 3.0 (Appendix 1)



4.3 MODEL DESCRIPTION

BAMGRO model is developed with input data files and various sub modules as explained below.

4.3.1 Input Data Files

The main inputs are daily weather data: as minimum temperature, maximum temperature, solar radiation, saturation deficit (*SD*) and rainfall. The major soil characteristics are soil bulk density and soil depth. These files were created from glasshouse experiments at Tropical Crops Research Unit (TCRU), University of Nottingham, UK and from field experiments in Africa (Chapter 3).

Landrace coefficients are the second main input file to BAMGRO. They were derived from various glasshouse (TCRU-Nottingham) and field experiments in Africa. The details of estimation of landrace coefficients and their values are explained in Chapters 5, 6 and 7.

4.3.2 Weather Module

The main role of the weather module is to read daily weather data from input files that were created using experimental measurements described in Chapter 3. It reads daily weather parameters (maximum and minimum air temperature, solar radiation, *SD*, rainfall in field sites and irrigation under controlled environmental experiments) from the weather files. In addition to the above mentioned parameters, relative humidity and wind speed are read from the weather file when available.

Thermal time is calculated hourly and integrated over the day (24 hours). This daily thermal time is used in the crop growth module to determine the accumulated phenochrons thereby the stage of growth. The accumulation of

thermal time over the growing period is calculated according to Eq. 4.3 as applied in BAMFOOD project model (Cornelissen, 2005).

$$T_{mean} = \frac{(T_{max} + T_{min})}{2} \quad 4.1$$

Hourly thermal time is accumulated over 24 h period using hourly temperature values $T_{d(i)}$

$$T_{d(i)} = T_{mean} + 0.5 \times abs(T_{max} - T_{min}) \times \cos(0.2618 \times (i - 14)) \quad 4.2$$

$$\frac{dT}{dt} = Min \left[\left(\frac{T_{d(i)} - T_{base}}{24} \right), 0 \right] \quad \text{for } i = 1, 24 \quad 4.3$$

Where,

T_{mean}	= daily mean temperature ($^{\circ}\text{C}$)
T_{min}	= daily minimum temperature ($^{\circ}\text{C}$)
T_{max}	= daily maximum temperature ($^{\circ}\text{C}$)
T_{base}	= base temperature ($^{\circ}\text{C}$)
T_{opt}	= optimum temperature ($^{\circ}\text{C}$)
$T_{d(i)}$	= hourly temperature in hour i ($^{\circ}\text{C}$)
TT	= cumulative thermal time (degree days)

4.3.3 Crop Growth Module

The accumulated thermal units produce the first leaf for the first instance and there after that rate of new leaf production (Eq.5.4) is dependent on daily accumulation of thermal time until maturity. Leaf area is produced as a function of leaf number (Eq. 5.15). Daily plant growth is computed by converting daily intercepted Photosynthetically Active Radiation (PAR) into

plant dry matter using a crop-specific radiation use efficiency parameter. The daily growth through light interception (Eq. 6.2) is computed as a function of LAI , radiation use efficiency (ϵ_s) and light extinction coefficient (k). The amount of new dry matter available for growth in each day is modified by the most limiting of soil moisture or solar radiation. Above ground biomass demands the major part of the carbohydrates produced each day and at the end of the day carbohydrates not used for above ground parts are allocated to roots, subjects to certain minimum requirements (Chapter 6).

The pod number (Eq. 6.19) is inversely proportional to the leaf number (Eq.5.3) with accumulation of thermal time; thereby a control is implicitly operated within the model to regulate pod formation. Once pod filling has started, the model computes the growth of pods based on user defined maximum rate. If the daily available photosynthates are insufficient to achieve the potential growth rate of pods, a fraction of carbohydrates can be remobilized from vegetative parts and roots to reproductive sinks each day based on demand of the reproductive organs (potential demand with priority function; Marcelis, 1993a). Pods are allowed to grow until physiological maturity provided sufficient resources for plant growth are available. If the growth resources are inadequate, growth is terminated prior to physiological maturity.

4.3.4 Soil Water Module

The BAMGRO-soil water module simulates root growth, root distribution, root water uptake and soil water balance from sowing until maturity for different bambara groundnut landraces. The soil is represented as a one dimensional profile; it is homogeneous horizontally and consists of number of soil layers. The total soil depth is assumed to be 1.5 m. This profile is divided into 15 soil layers each of 10 cm depth. The details of the soil water module, calibration and validation results are explained in Chapter 7.

Water stress index

For the purpose of the model it is assumed that growth of the unstressed crop is limited by the solar radiation available for photosynthesis process and its photosynthetic capacity. This is defined as light limited growth (*LLG*). When the growth is reduced by water limitation this is termed as water limited growth (*WLG*). If the crop is exposed to a restriction of water supply and the water uptake by roots is insufficient to replenish transpiration at potential growth rates the plant is exposed to moisture stress. The BAMGRO model contains a number of relationships in which the growth and developmental performances of the crop are modified by the water stress that is experienced. To model the effect of soil moisture stress on growth and development, water balance and a relation between crop growth and water availability is considered. The value is given from zero to one, representing maximum stress and no stress respectively. The basis of calculation of water stress index was derived from BAMnut (Bannayan, 2001) and modified for present model BAMGRO.

$$WSTRESS = \left(\min \left(\frac{WLG}{LLG} \right), 1 \right) \quad 4.4$$

Where,

<i>WSTRESS</i>	= water stress index
<i>WLG</i>	= water limited growth (Eq.7.6)
<i>LLG</i>	= light limited growth (Eq. 6.2)
<i>T_{high}</i>	= ceiling temperature (°C)

4.3.5 Temperature Module

The temperature sub module considers the output from the weather module as input to calculate temperature stress index according to Eqs. 4.5 and 4.6 depending on the mean temperature. When the crop is exposed to a range of temperature within the boundary line of base (T_{base}) and ceiling (T_{high}) temperatures, it results in temperature stress effects on growth and development. However temperature stress can be further divided into heat and cold stress based on the mean temperature and agro-ecological adaptation of the landrace (Chapter 8). Similar to *WSTRESS* the value of temperature stress index ranges between zero (maximum stress) and one (no stress) (Figure 4.2).

$$TSTRESS = \frac{(T_{mean} - T_{base})}{(T_{lower} - T_{base})} \quad \text{for } T_{mean} \leq T_{lower} \quad 4.5$$

$$TSTRESS = \frac{(T_{mean} - T_{upper})}{(T_{high} - T_{upper})} \quad \text{for } T_{mean} > T_{upper} \quad 4.6$$

Where,

$TSTRESS$ = temperature stress index.

T_{high} = ceiling temperature ($^{\circ}\text{C}$)

T_{lower} = lower threshold level of temperature ($^{\circ}\text{C}$)

T_{upper} = upper threshold level of temperature ($^{\circ}\text{C}$)

BAMGRO calculates temperature stress index according to Eqs. 4.5 and 4.6, and two threshold levels are set as lower (T_{lower}) and upper (T_{upper}) for each landrace as a novel approach in present study. When T_{mean} is lower than the T_{lower} crop experience a cold stress while temperatures above T_{upper} it causes a heat stress (Figure 4.2). Based on the experimental evidences in glasshouse experiment (TCRU-2006) the lower and upper threshold levels for Swaziland landrace, Uniswa Red are set as 17 $^{\circ}\text{C}$ and 35 $^{\circ}\text{C}$ respectively. However, the

Namibian landrace, S19-3 reported a cold stress with LT (23 ± 5 °C) while no significant heat stress with HT (33 ± 5 °C) and therefore, BAMGRO uses 24 °C and 38 °C for lower and upper threshold levels.

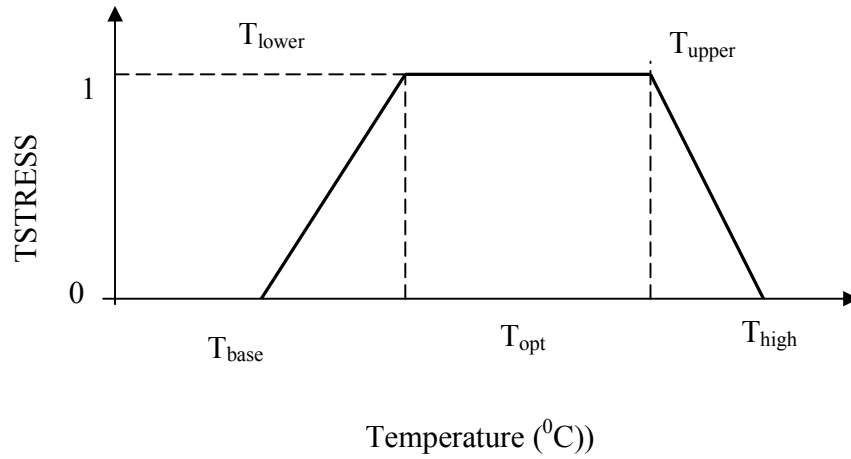


Figure 4.2. Diagrammatic representation of variation in temperature stress index (*TSTRESS*).

4.3.6 Photoperiod Module

Bambara groundnut is a short day crop and pod formation is regulated by photoperiod (Linnemann and Craufurd, 1994; Brink, 1997). The experimental evidence from growth room experiments at the University of Copenhagen, Denmark, showed that photoperiod is positively correlated with rate of leaf production (Figure 5.2). Therefore BAMGRO calculates the day length factor to adjust the daily rate of change in new leaf production (Eq.5.4) when the crop is grown above 12 h day length. The gradient of the linear function of rate of leaf production with different day lengths is simply considered as the day length factor (DL_{fac}) (Eqs. 4.7, 4.8) as a new approach in BAMGRO model.

$$DL_{fac} = 1 \quad \text{for } DL \leq 12 \text{ h} \quad 4.7$$

$$DL_{fac} = p_1 \times DL \quad \text{for } DL > 12 \text{ h} \quad 4.8$$

Where,

DL = day length (h)

DL_{fac} = day length factor

p_1 = landrace parameter (Table 5.1)

4.4 BAMGRO RESPONSE TO ABIOTIC STRESS

Environmental stresses represent the most limiting factors for agricultural productivity. Apart from the biotic stress caused by plant pathogens, there are number of abiotic stresses such as extremes in temperature, drought, salinity, heavy metals and radiation which all have detrimental effects on plant growth and yield. However certain plant species and ecotypes have developed various mechanisms to adapt such stress conditions (Hirt et al., 2004). According to the evidences from TCRU-experiments (Table 3.4), bambara groundnut reported that growth, development and yield are impaired by abiotic stress factors. The present study considers soil moisture and temperature as major abiotic stress factors that influence growth and yield of bambara groundnut. Depending on the timing, severity, duration and landrace the type of stress varies for different plant processes (Table 3.4). BAMGRO model distinguishes three stress effects due to independent and cumulative effects of drought (*WSTRESS*) and temperature stress (*TSTRESS*) as: on leaf production (Ks_1 ; Eq. 5.5 and 5.6), leaf senescence (Ks_2 ; Eq.5.13) and dry matter partitioning (Ks_3 ; Eq.4.4). These stress indices are modifiers of the target model parameters and varies in value from one when the effect is non-existent, to zero when the effect is maximum.

4.5 MODELLING SOFTWARE: Model Maker 3.0

BAMGRO model is formulated and run using the Model Maker software (Version 3.0). This uses a simple drag and drop approach to simulation modelling and is more intuitive and added extra features to improve optimisation and analysis. The software provides facilities to formulate the model using differential functions, conditional applications, time triggers events and run the model on user defined time steps. The coding of BAMGRO in Model Maker is presented in Appendix 1 (Model Maker manual).

4.6 EFFICIENCY CRITERIA

In order to assess model performances and provide an objective evaluation of the “closeness” of simulated (S) vs. measured (M) values, a number of indicators are used. There are different goodness-of-fit measures and they will each be sensitive to different aspects of model (mis) behaviour (Wainwright and Mulligan, 2002). However the choice of an appropriate measure is important in robust model evaluation.

4.6.1 Visual Evaluation

This is used to evaluate in a subjective way model performance, especially related to systematic behaviour (under or over estimation).

4.6.2 Gradient (b) and Intercept (a) of The Linear Regression

This involves an analysis of the simulated (S_i) and measured (M_i) values.

$$S_i = a + b \cdot M_i \quad 4.9$$

Simple t-test is performed to check the significant deviations of slope of the regression line (a) and the intercept (b) from the ideal line of identity (1:1) in which the slope is one and intercept is zero.

4.6.3 The Nash and Sutcliffe (N-S) (1970) Model Efficiency Measure

$$N - S = 1 - \frac{\sum_{i=1}^n (M_i - S_i)^2}{\sum_{i=1}^n (M_i - \overline{M})^2} \quad 4.10$$

N-S is the measure of the mean square error to the observed variance. If the error is zero, then N-S=1, and the model represents a perfect fit. If the error and observed variance are equal, then N-S=0 and the observed mean value is as a good representation of the model. A negative N-S value indicates that the error about the model is greater than the error about the mean (very poor fitting model).

4.6.4 Mean Absolute Error (MAE)

This is the mean absolute deviation between the simulated (S_i) and measured (M_i) values.

$$MAE = \frac{\sum_{i=1}^n |M_i - S_i|}{n} \quad 4.11$$

4.7 CHAPTER SUMMARY

- The main model BAMGRO is comprised sub modules for weather, crop growth, soil water, temperature and photoperiod.
- The weather module initiates the model run by reading daily weather parameters from the input files and calculates thermal units for the crop growth and developmental processes.
- The crop growth module predicts the growth of roots (*RW*), leaves (*LW*), stems (*STEMW*) and pods (*PW*) depending on the prevailing environmental conditions.
- The soil water sub module is mainly responsible for the prediction of soil moisture levels to decide whether the crop is water limited or not. The moisture stress index (*WSTRESS*) is computed considering *WLG* and *LLG*.
- The temperature module calculates the *TSTRESS* as a function of cardinal temperatures
- The photoperiod module computes the day length factor (*DL_{fac}*) to modify the rate of new leaf production and thereby control the rate of change in pod number when the crop is grown above 12 h day length.

CHAPTER 5

5.0 MODELLING CANOPY DEVELOPMENT OF BAMBARA GROUNDNUT FOR ABIOTIC STRESS

5.1 INTRODUCTION

Canopy development is a fundamental process in crops as leaves intercept solar radiation and produce carbohydrates through photosynthesis. Appearance, expansion and senescence of individual leaves are critical determinants of canopy development and thereby crop productivity. Information on canopy development is important in breeding programmes where crop morphology is a widely used selection criteria.

The first dynamic model for bambara groundnut, BAMnut simulated the canopy expansion as a function of thermal time and senescence through phenological stages and water limitation (Bannayan, 2001). Conceptual carbohydrate pools for total canopy (leaves and stem mass) are computed by way of shoot to root ratio calculated from experimental evidence. Leaf carbohydrate content is derived by using a fixed ratio between leaf area to dry mass (Specific Leaf Area- SLA ; $\text{cm}^2 \text{g}^{-1}$).

The model developed in BAMFOOD project (Cornelissen, 2005), simulated the canopy development of bambara groundnut with linear functions between new leaf production (Eq. 5.1) and phenochrons (Matthews and Stephens, 1998a), between leaf number and potential leaf area per plant per phenochrons (Eq. 5.2) and senescence fractions due to shading, soil moisture and temperature. The model uses a multiplier (WM_2) that ranges from zero to one, to modify the rate of leaf area expansion due to drought assuming canopy development under water limited conditions can be regulated by leaf area expansion only.

$$N_i = p_i \times N_{ph} \quad 5.1$$

Where,

- N_i = total number of leaves (plant⁻¹)
 p_i = phyllochron (number of leaves plant⁻¹ phenochron⁻¹)
 N_{ph} = number of accumulated phenochrons

$$\frac{dLA}{dt} = (k \times N_i) + \lambda \quad 5.2$$

Where,

- LA = leaf area (cm² plant⁻¹ phenochron⁻¹)
 k = landrace coefficient (cm² plant⁻¹)
 λ = landrace coefficient (cm² plant⁻¹ phenochron⁻¹)

Validating the above model for water limited conditions for field experiment in Luve, Swaziland Cornelissen (2005) found that the model greatly overestimated *LAI* during the initial growth stages. The lack of a slowing effect of drought on leaf production was considered as the primary reason for the discrepancies between simulated and measured *LAI*.

Bambara groundnut exhibits a considerable degree of phenotypic diversity in morphology, growth habit and crop duration between landraces including canopy development (Linnemann and Azam-Ali, 1993; Collinson et al., 1996; 1997). Little effort has been focussed on modelling canopy development for different landraces under the major abiotic stresses (drought, heat and cold), presumably due to lack of suitable modelling approaches and unavailability of data sets.

The present study develops the model framework to simulate the canopy expansion more comprehensively when the crop is exposed to variable climatic conditions. The new model, BAMGRO uses a novel approach to simulate the rate of leaf appearance by describing the rate of new leaf production as a Gaussian

function of cumulative thermal units. Leaf area expansion is then simulated as a linear function of leaf number. The senescence fraction is calculated from the phenological stage, temperature, shading effect and soil moisture. In addition, the model uses a modifier to adjust the rate of leaf appearance based on soil moisture (*WSTRESS*) and temperature (*TSTRESS*).

Therefore, the main objectives of the current study were to (1) obtain experimental data on the time course of canopy expansion of bambara groundnut landraces at different air temperatures under limiting and non-limiting soil moisture regimes and (2) develop new functions for the rate of new leaf production, leaf expansion and senescence under variable climatic conditions.

The model development is explained in section 5.2 together with suitable canopy development data and parameterisation results. This is followed by model validation results (section 5.3) and the Chapter summary (section 5.4).

5.2 MODEL DEVELOPMENT AND PARAMETERISATION

5.2.1 Leaf Appearance

Bambara groundnut is an indeterminate crop so leaf appearance can occur from emergence until maturity, depending upon the supply of assimilates available for leaf growth, photoperiod and the effect of stress due to drought and temperature. A fraction of produced leaves is removed from the plants as dead leaves. This senescence fraction is dependent upon the phenological stage and the abiotic stress factors. Therefore the actual leaf number can be explained as the balance between the rate of new leaf production and the rate of leaf senescence (Eq.5.3).

$$\frac{dLN}{dt} = (LN_{new}) - (LN_{dead}) \quad 5.3$$

Where,

$$\begin{aligned} LN &= \text{actual leaf number plant}^{-1} \\ LN_{new} &= \text{new leaf number plant}^{-1} \text{ d}^{-1} \text{ (Eq. 5.4)} \\ LN_{dead} &= \text{dead leaf number plant}^{-1} \text{ d}^{-1} \text{ (Eq. 5.14)} \end{aligned}$$

A logistic function was fitted for the glasshouse data (TCRU experiment 2002; 28 ± 5 °C, TCRU experiment 2006; 23 ± 5 °C and 23 ± 5 °C, University of Nottingham, UK) using Genstat 8.1 to describe the new leaves produced per cumulative thermal units. This relationship was used to calculate the daily rate of leaf production which was then described by a Gaussian function (Eq.5.4) (Figure 5.1). According to the experimental results, the rate of new leaf production is depend on, day length (DL_{fac}), abiotic stress (Ks_I) and plant population ($Densityfac$). Therefore the rate of new leaf production is described by following Eq. 5.4.

$$LN_{new} = \left\{ a \times Ks_I \times Densityfac \times \exp \left[-\frac{(TT - b)^2}{(c)^2} \right] \right\} \times \Delta TT_i \times DL_{fac} \quad 5.4$$

Where,

$$\begin{aligned} TT &= \text{cumulative thermal time (degree days)} \\ \Delta TT_i &= \text{daily thermal time (degree days d}^{-1}\text{)} \\ a, b, c &= \text{landrace coefficients (Table 5.1)} \\ Ks_I &= \text{stress index on leaf production (Eq. 5.5, Eq. 5.6)} \\ Densityfac &= \text{density factor (Eq. 5.7)} \end{aligned}$$

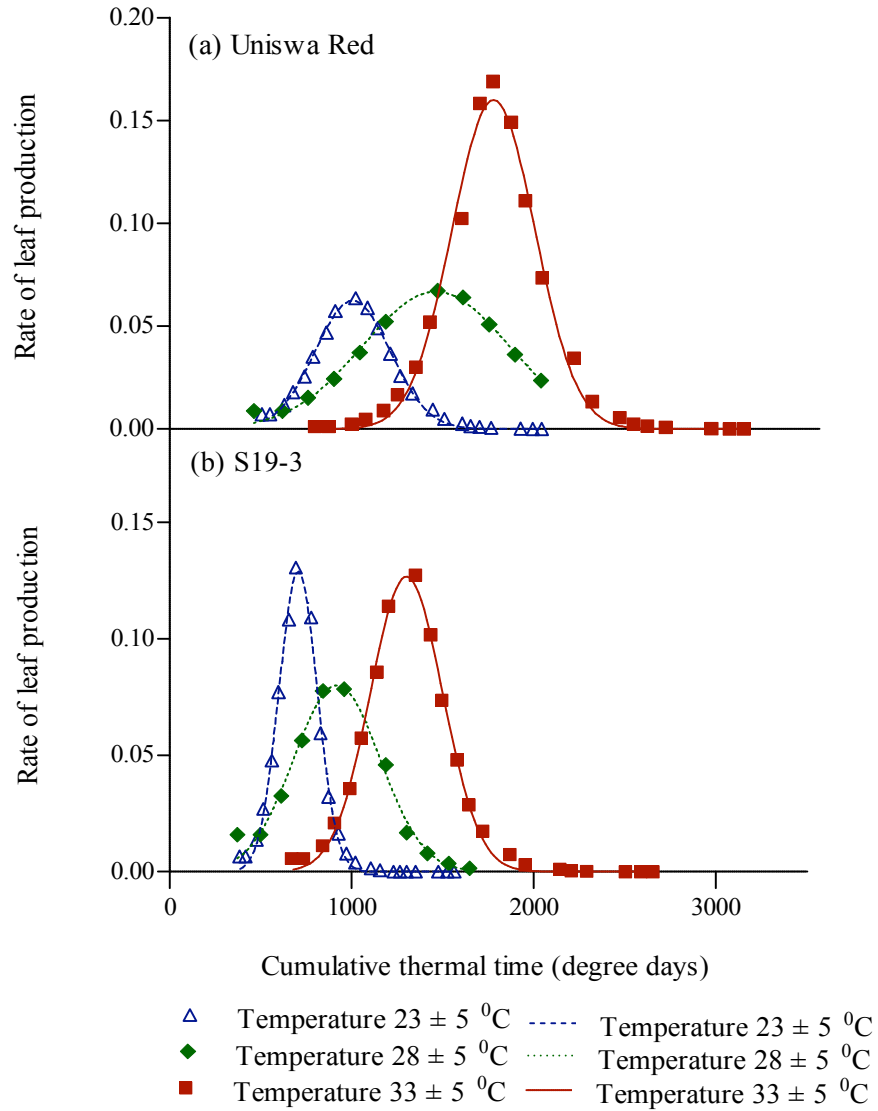


Figure 5. 1. Corresponding measured (symbols; calculated from fitted logistic function) and simulated (lines) for the rate of new leaf production with cumulative thermal time in landraces, Uniswa Red (a) and S19-3 (b) grown at low temperature (23 ± 5 °C), ‘optimum’ temperature (28 ± 5 °C) and high temperature (33 ± 5 °C): TCRU glasshouse experiment 2002 and 2006. Measured data are the average of ten (28 ± 5 °C), twenty (23 ± 5 °C) and thirty (33 ± 5 °C) plants per landrace (standard deviations not shown to improve the clarity). Simulated lines were obtained using Gaussian function (Eq. 5.4) with parameters and correlation coefficients in Table 5.1.

The relative response of rate of leaf production in tested two landraces (Uniswa Red and S19-3) implies that both landraces exhibit similar responses to optimum temperature but differently to extremes (low temperature: 23 ± 5 °C and high temperature 33 ± 5 °C). Comparison of the coefficients for Uniswa Red and S19-3 (Table 5.1) indicated that linear terms were significantly different. This information is used as a key to set heat and cold stress on rate of leaf production in Uniswa Red and S19-3.

Rate of new leaf production is affected by photoperiod, abiotic stress factors (drought, heat and cold) and the plant population as per details below. A positive correlation between day length and the rate of new leaf production was observed in controlled environment experiments (growth room) in the University of Copenhagen, Denmark. The variation of the rate of leaf production with increasing photoperiod is shown in Figure 5.2. The slope (p_l - Table 5.1) of the linear function at 60 DAS is used to calculate the day length factor for two landraces (Uniswa Red and S19-3) when they are grown at day lengths greater than 12 h (Eq.4.8).

In addition, the effect of major abiotic stress on the rate of leaf appearance is explained by a modifier K_{s_l} . This is calculated considering the temperature stress and water stress as a novel approach in BAMGRO model.

$$K_{s_l} = \text{Min}(WSTRESS, 1) \quad \text{for } T_{mean} > T_{upper} \quad 5.5$$

$$K_{s_l} = \text{Min}(TSTRESS, WSTRESS) \quad \text{for } T_{mean} \leq T_{lower} \quad 5.6$$

Where,

$WSTRESS$ = drought stress (Eq. 4.4)

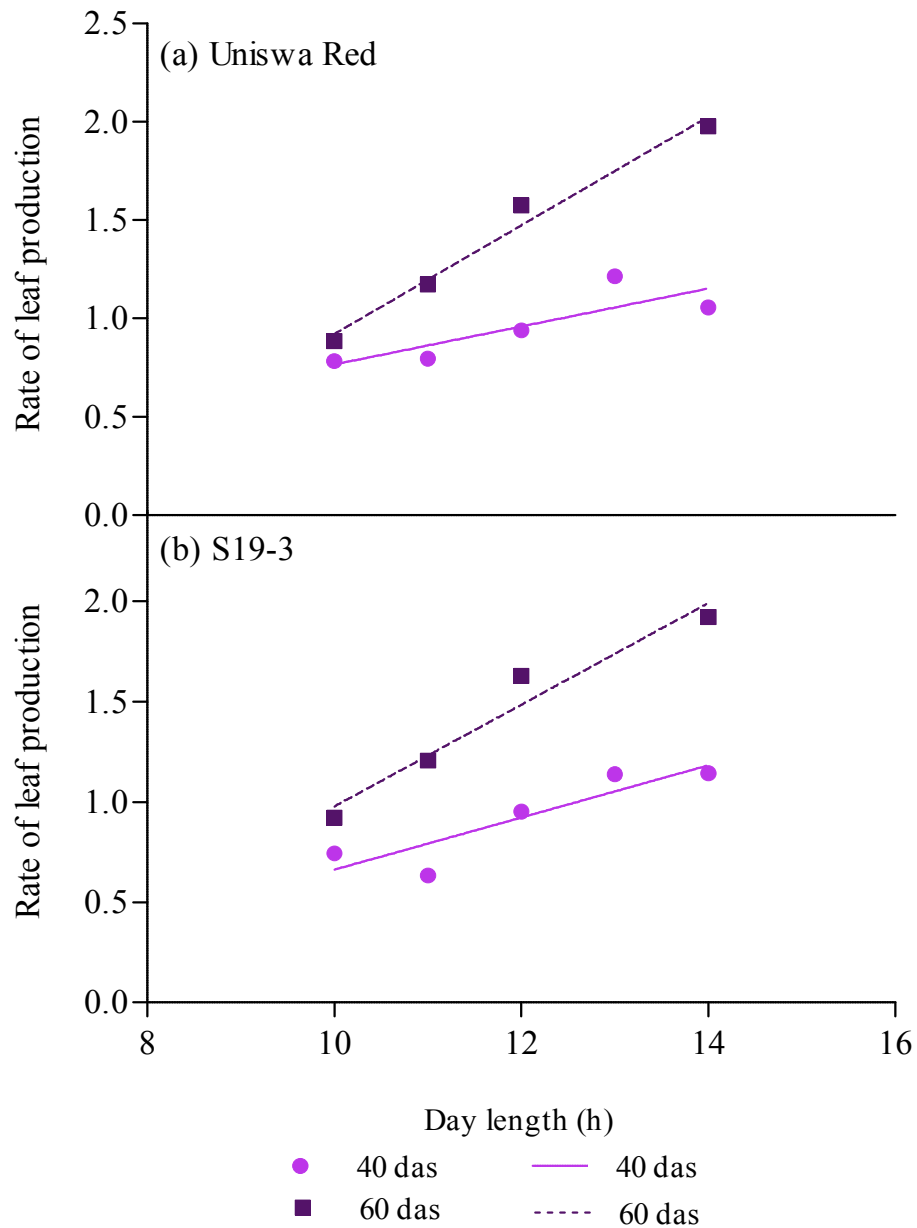


Figure 5. 2. Regression of rate of leaf appearance against day lengths for two bambara groundnut landraces grown under day lengths (10 h, 11 h, 12 h, 13 h, 14 h) in growth chambers: 40 DAS and 60 DAS: (a) Uniswa Red (b) S 19-3. The regression equations for Uniswa Red are $Y = 0.096 \times DL - 0.19$, $r^2 = 0.70$; $Y = 0.27 \times DL - 1.84$, $r^2 = 0.97$ at 40 DAS and 60 DAS respectively. The regression equations for S19-3 are $Y = 0.13 \times DL - 0.63$, $r^2 = 0.80$; $Y = 0.25 \times DL - 1.55$, $r^2 = 0.95$ at 40 DAS and 60 DAS respectively.

A negative correlation was observed for rate of leaf production and the plant density for Botswana field data therefore density factor was calculated relative to the density of TCRU experiments (Eq. 5.7).

$$Densityfac = \frac{TCRU_{density}}{density} \quad 5.7$$

Where,

$TCRU_{density}$ = plant density in TCRU experiment (15 plants m⁻²)
 $density$ = number of plants m⁻²

5.2.2 Leaf Senescence

BAMGRO calculates a base level of senescence due to the environmental factors which is subsequently adapted according to the stress level on a daily basis. The model calculates a senescence fraction due to physiological maturity, shading (low light intensity), temperature (heat and cold stress), and drought stress. The basis of senescence due to shading, temperature and soil moisture is similar to BAMFOOD project model and modified for the present model BAMGRO with parameter values derived from TCRU-2006 experiment by means of model optimisation.

When phenological stage is at flowering

$$Sen_{PHY} = 0.01 \quad 5.8$$

Where,

Sen_{PHY} = senescence fraction due to physiological maturity of leaves

$$Sen_L = Max(Min((0.05 \times (LAI - 3)), 1), 0) \quad \text{for } T_{mean} \leq T_{opt} \quad 5.9$$

$$Sen_L = Max(Min((0.1 \times (LAI - 5)), 1), 0) \quad \text{for } T_{mean} > T_{opt} \quad 5.10$$

Where,

Sen_L = senescence fraction due to mutual shading

In the absence of temperature and water stress, leaf senescence is exclusively due to physiological maturity and mutual shading.

$$Sen_T = Max(Min((TSTRESS \times 0.01), 1), 0) \quad 5.11$$

Where,

Sen_T = senescence fraction due to temperature stress

$$Sen_W = Max(Min((WSTRESS \times 0.1), 1), 0) \quad \text{for } 0 \leq WSTRESS \leq 1 \quad 5.12$$

Where,

Sen_W = senescence fraction due to water stress

The overall fractional rate of leaf senescence is Ks_2 (d^{-1}) and taken as the maximum value of Sen_{PHY} , Sen_L , Sen_T and Sen_W .

$$Ks_2 = Max(Sen_{PHY}, Sen_L, Sen_T, Sen_W) \quad 5.13$$

Ks_2 is used to calculate leaf senescence (Eq. 5.14)

$$LN_{dead} = LN_{new} \times Ks_2 \quad 5.14$$

The model calibration results for number of leaves per plant for the tested two landraces (Uniswa Red and S19) that are calculated by Eq. 5.3 are shown in Figure 5.3. The accuracy and proper functioning of BAMGO model for leaf production under temperature stress was tested with temperature stress function switch off ($TSTRESS=1$, Eq. 4.5 and 4.6) and simulation results are shown in Figure 5.3. Swaziland landrace Uniswa Red explains the significantly lower leaf production when $TSTRESS=1$ (no heat stress) whereas in Namibian landrace, S19-3, no reduction. Also both landraces reported higher leaf production when the model assumes no $TSTRESS$ (no cold stress) and it was relatively higher in S19-3 compared to Uniswa Red (Figure 5.3). The results clearly show the behaviour of BAMGO model for leaf production under temperature stress.

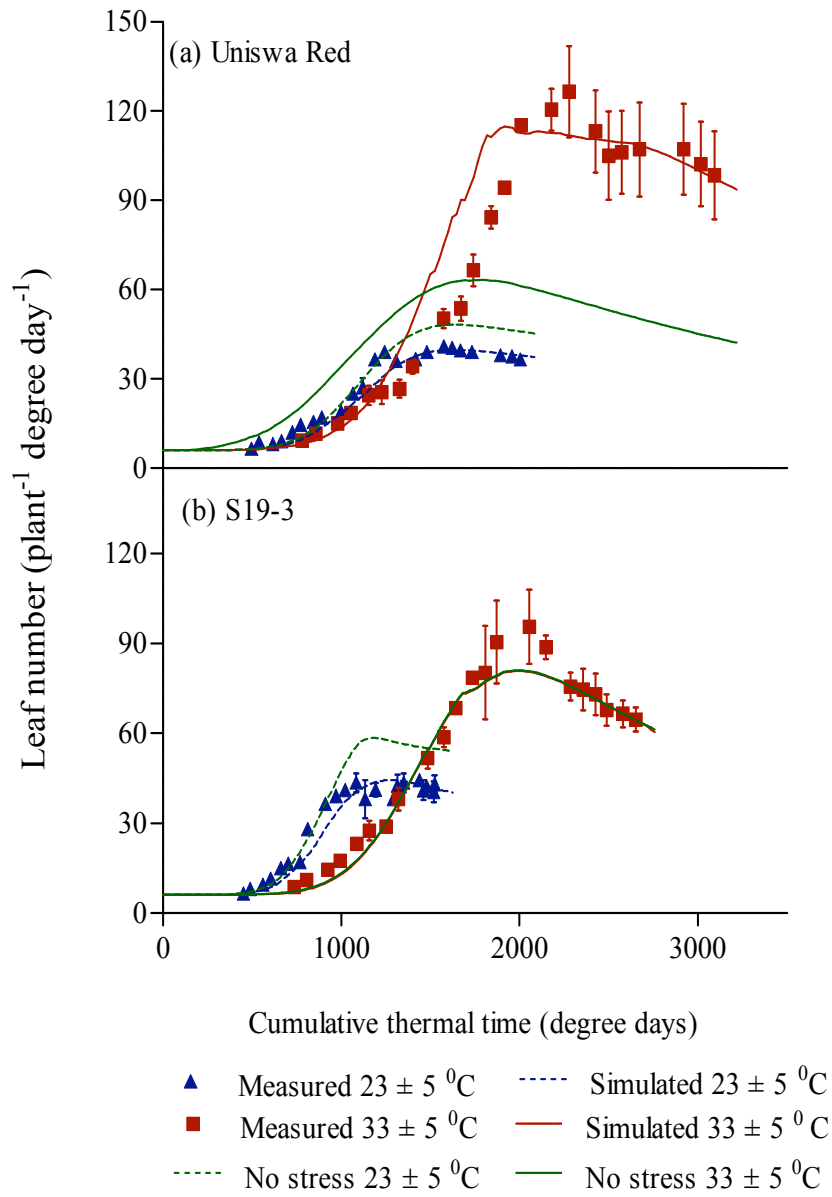


Figure 5. 3. Model calibration for leaf production with cumulative thermal time in landraces, Uniswa Red (a) and S19-3 (b) grown at low temperature ($23 \pm 5^\circ\text{C}$) and high temperature ($33 \pm 5^\circ\text{C}$): TCRU glasshouse experiment 2006. Measured data are the average of twenty ($23 \pm 5^\circ\text{C}$) and thirty ($33 \pm 5^\circ\text{C}$) plants per landrace. The simulation results with no stress ($TSRESS=1$) are shown with calibration results for LT and HT. Vertical bars are standard error (\pm SE). Simulated lines were obtained by Eq. 5.3 with parameters and correlation coefficients in Table 5.1.

5.2.3 Leaf Expansion

BAMGRO calculates the leaf area using the current leaf number (as calculated in Eq. 5.3) together with a fitted relation with leaf area per individual leaf (Eq. 5.15). This relationship was derived from TCRU-2006 experiment and the major assumption in calculating the leaf area is uniform size in individual leaf irrespective of the age of the leaf. Therefore, BAMGRO uses a single coefficient LA_l (Table 5.1) to estimate leaf area expansion and finally leaf area index (LAI) as in Eq. 5.16.

$$LA = LA_l \times LN \quad 5.15$$

$$LAI = \frac{LA \times Density}{10000} \quad 5.16$$

Where,

LA = leaf area ($\text{cm}^2 \text{ plant}^{-1}$)

LAI = leaf area index of the canopy

LA_l = landrace coefficient for leaf area expansion

The LAI calibration results for two landraces, Uniswa Red and S19-3 grown at low and high temperatures that is calculated by Eq. 5.16 are shown Figure 5.4. Similar to leaf production function, LAI simulations with no $TSTRESS$ are included in Figure 5.4.

Table 5.1 Landrace specific parameters used for the calculation of leaf number, leaf area and $DLfac$ for two landraces (Uniswa Red and S19-3) (Values based on TCRU glasshouse experiment 2002, 2006 and growth room experiment in Copenhagen University, Denmark). Parameter values of S19-3 were adjusted for DipC and OM1.

Landrace coefficients	Uniswa Red	S19-3	DipC	OM1
a	0.075	0.13	0.12	0.12
b	1100	900	900	900
c	260	200	200	200
LA_l -glasshouse	33	35	40	40
LA_l -field Botswana	17	17	20	20
p_l	0.27	0.25	0.25	0.25

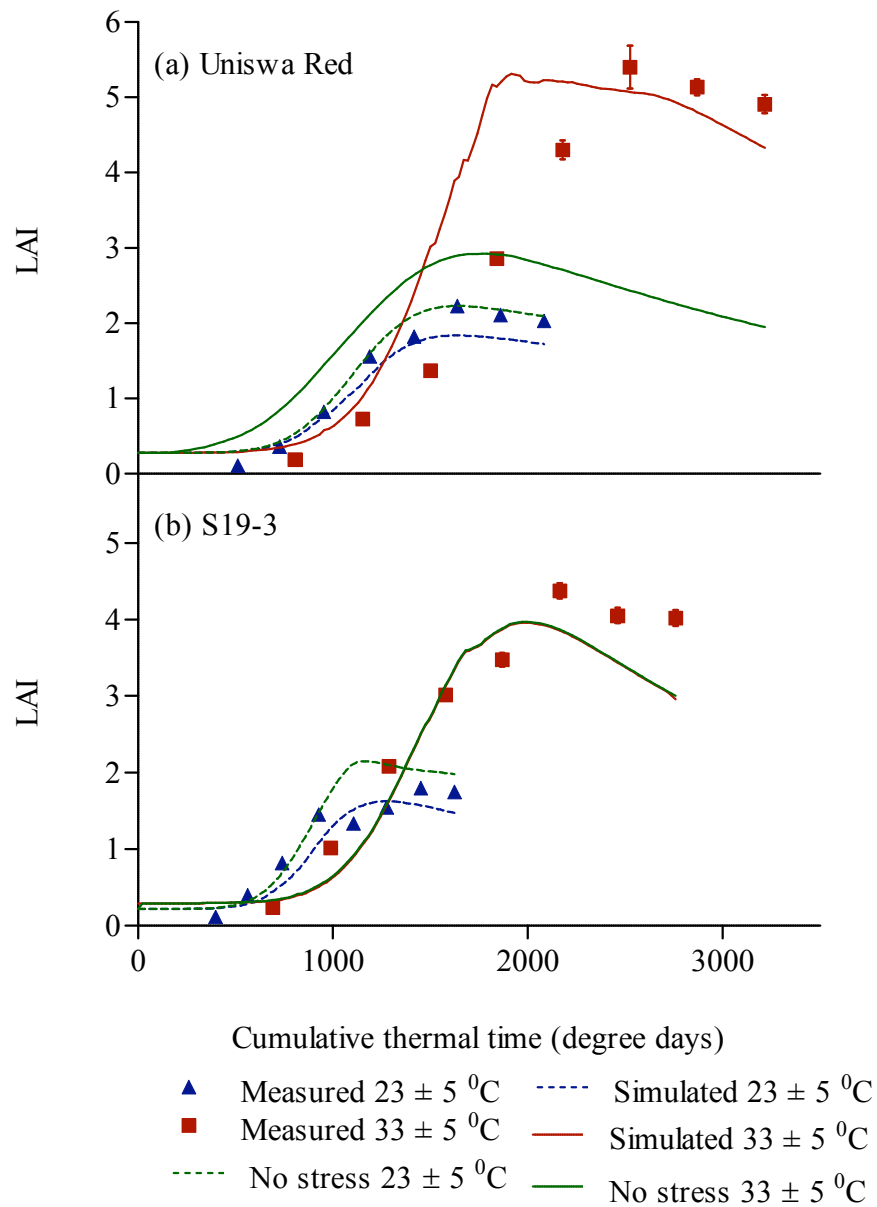


Figure 5. 4. Model calibration for *LAI* with cumulative thermal time in landraces, Uniswa Red (a) and S19-3 (b) grown at low temperature (23 ± 5 °C) and high temperature (33 ± 5 °C): TCRU glasshouse experiment 2006. Measured data are the average of twenty (23 ± 5 °C) and thirty (33 ± 5 °C) plants per landrace. The simulation results with no stress ($TSRESS=1$) are shown with calibration results for LT and HT. Vertical bars are standard error (\pm SE). Simulated lines were obtained using Eq. 5.16 with parameters and correlation coefficients in Table 5.1.

5.3 MODEL VALIDATION

The canopy development model was validated using the values for leaf number per plant (Eq. 5.3) and *LAI* (Eq. 5.16) for two landraces (Uniswa Red and S19-3) grown under glasshouse condition (TCRU-2007 and TCRU-2008) and three landraces (Uniswa Red, DipC and OM1) grow in field sites in Botswana and Swaziland.

5.3.1 Leaf Appearance

Experimentally the rate of leaf production varied with the daily mean temperature and reduced with drought in both landraces and this is well described by the model.

The model predictions for glasshouse experiments (2007 and 2008), show that both Uniswa Red and S19-3 reduced the rate of leaf production significantly with decreasing temperature LT (23 ± 5 °C) exhibiting the adjustments to the rate of new leaf production (Eq. 5.4) and the rate of senescence (Eq. 5.14) through cumulative stress coefficients Ks_1 and Ks_2 respectively (Figure 5.5). The statistical results (N-S and MAE) for the model comparison are summarised in Table 5. 2. Simulated leaf number per plant correlated well with glasshouse measurements for Uniswa Red for considered two years (2007 and 2008) with higher N-S (ranges from 0.76 to 0.92) and lower MAE (± 2.91 to 3.98). However the simulation results for Uniswa Red under HT (33 ± 5 °C) in 2007 reported poor correlation with lower N-S (0.42) and higher MAE (± 20.25) during the middle part of the growth cycle (Figure 5.5). The model comparison of leaf number for S19-3 reported relatively lower N-S (ranges from 0.49 to 0.82) and higher MAE (± 4.96 to 10.11) compared to Uniswa Red. Similar to Uniswa Red, the weakest correlation was reported for S19-3 in 2007 experiment but under LT (Table 5.2). However the model simulation results for the leaf number followed the general trend of measured values throughout for both landraces with minor deviations coincided with peak values.

The rate of leaf production varied with the sowing dates as it is connected to the day length mainly and the model successfully simulates the effect of photoperiod on leaf production using the day length factor (Figure 5.6) for 2 sowing dates in field sites in Notwane, Botswana. However the model comparison with measured values reported that N-S ranges from 0.24 to 0.74 with MAE (\pm 6.18 to 13.4) for the crop sown on 1 February 2007. Since BAMGRO was primarily parameterised for Uniswa Red and S19-3, the simulation results for Uniswa Red (N-S, 0.74, February 1; 0.88, January 18) are better than that for DipC (N-S, 0.24, February 1; 0.83, January 18) and OM1 (N-S, -0.42, February 1; 0.86, January 18). Although the measured values are scattered around simulated lines, BAMGRO simulates the trend in leaf production successfully for two sowing dates in Botswana field sites explaining the effect of major abiotic stress.

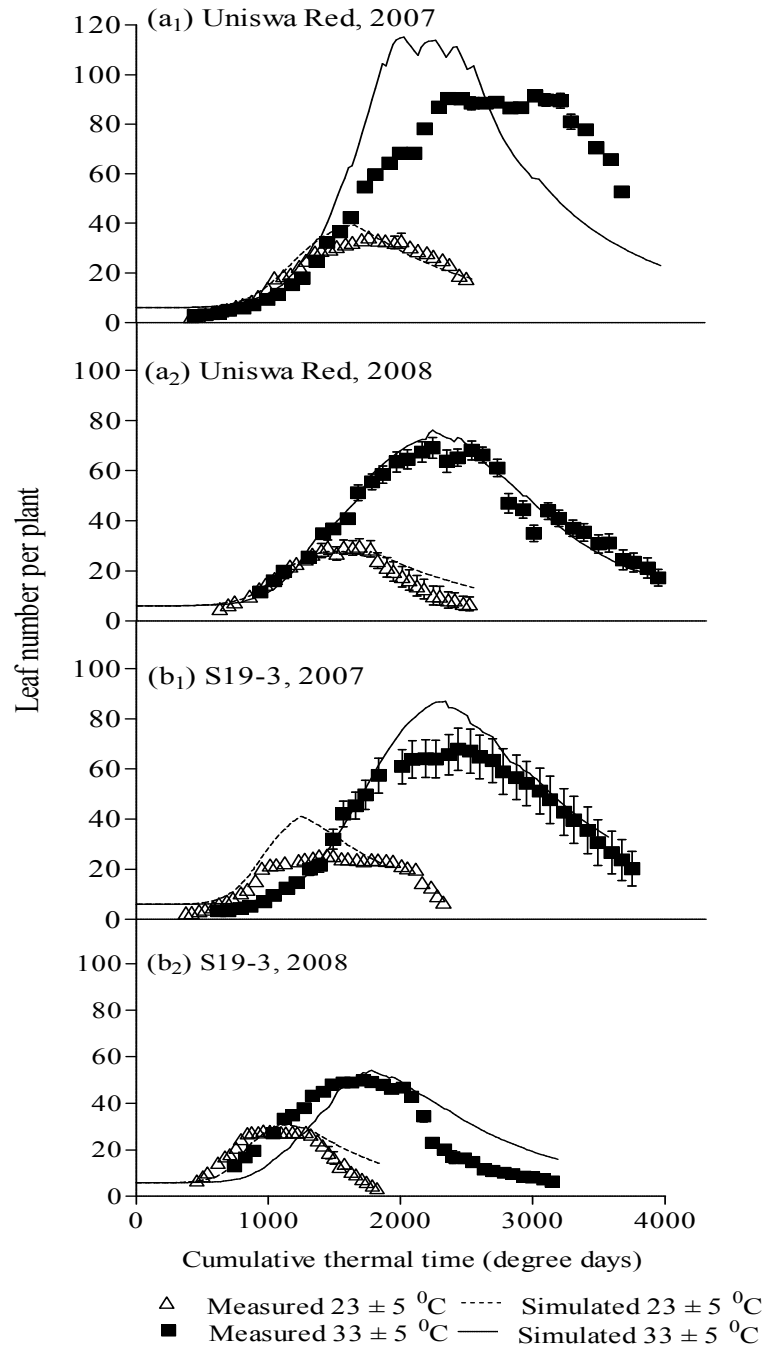


Figure 5. 5. Validation of leaf number per plant with cumulative thermal time grown under glasshouse conditions for two bambara groundnut landraces Uniswa Red (a₁, a₂), S19-3 (b₁, b₂) with drought at 77 DAS (TCRU 2007 experiment) and 33 DAS (TCRU-2008 experiment) respectively. Measured data are the average of twenty (23 ± 5 °C) and thirty (33 ± 5 °C) plants per landrace. Vertical bars are standard error (\pm SE).

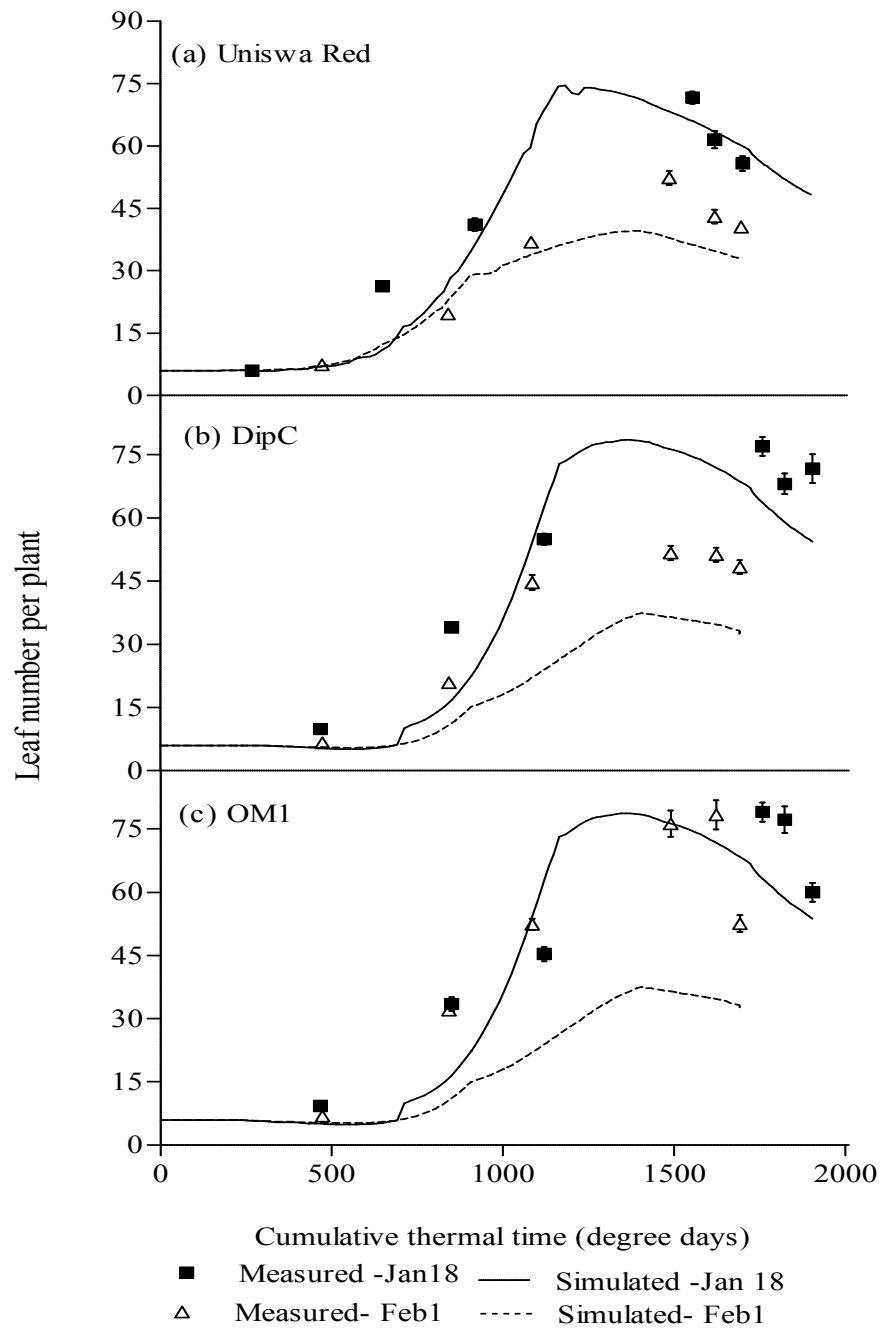


Figure 5. 6. Validation of leaf number per plant measured at field sites in Botswana for two sowing dates: January 18 and February 1 in growing season 2006/2007 for three bambara groundnut landraces (a) Uniswa Red (b) DipC (c) OM1. Measured data are the average of six plants per landrace. Vertical bars are standard error (\pm SE).

Table 5.2. Comparison of leaf number model predictions with experimental data for glasshouse (TCRU), Sutton Bonington Campus, University of Nottingham, UK and field sites in Notwane, Botswana.

Location/Experiment Treatment	Period	Number of observations	N-S	MAE
TCRU-glasshouse				
Uniswa Red: 23 ± 5 °C	2007	36	0.89	3.09
Uniswa Red: 33 ± 5 °C	2007	36	0.42	20.25
S91-3 : 23 ± 5 °C	2007	36	-0.10	3.77
S91-3 : 33 ± 5 °C	2007	36	0.82	7.34
TCRU-glasshouse				
Uniswa Red : 23 ± 5 °C	2008	32	0.76	2.91
Uniswa Red: 33 ± 5 °C	2008	32	0.92	3.98
S91-3 : 23 ± 5 °C	2008	32	0.52	4.96
S91-3 : 33 ± 5 °C	2008	32	0.49	10.11
Botswana				
Uniswa Red: Jan 18	2007	06	0.88	5.9
Uniswa Red: Feb1	2007	06	0.74	6.18
DipC : Jan 18	2007	06	0.83	8.29
DipC : Feb1	2007	06	0.24	13.49
OM1 : Jan 18	2007	06	0.86	6.7
OM1 : Feb1	2007	06	-0.42	26.09

5.3.2 Leaf Expansion

LAI varied with temperature, soil moisture and sowing dates (photoperiod), which the model successfully described (TCRU: Figure 5.7; Botswana: Figure 5.8; Swaziland: Figure 5.9). As for leaf number, two landraces (Uniswa Red and S19-3) under glasshouse condition, Nottingham and three landraces (Uniswa Red, Dip C and S19-3) for field sites in Botswana and Swaziland (Luve, Malkerns) were tested for *LAI*. The results of statistical analysis for the model comparison for *LAI* with 1:1 line are given in Table 5.3.

Experimentally, both landraces, S19-3 and Uniswa Red showed an increase in *LAI* with increasing temperature (HT) with wider gap between HT and LT in Uniswa Red exhibiting heat stress on rate of leaf production thereby on leaf area expansion. Similar to the rate of leaf production, drought reduced the *LAI* in both landraces. This variation in canopy development is simulated successfully by BAMGRO (Figure 5.7). *LAI* correlated well with glasshouse measurements for Uniswa Red for 2 years (2007 and 2008) with higher N-S (ranges from 0.74 to 0.87) and lower MAE (± 0.20 to 0.28). The poor correlation in rate of leaf appearance in HT during 2007 season was consistent with simulation results of *LAI* (N-S, 0.13 and MAE, ± 1.27). S19-3 reported a good fit to the observed values in all the treatments (2007 and 2008) with higher N-S (ranges from 0.55 to 0.87) and lower MAE (± 0.20 to 0.50).

LAI varied with date of sowing in field experiments as it is a function of leaf number and the model simulates the variation of *LAI* for two sowing dates (January 18, February 1) tested in Botswana (Figure 5.8). BAMGRO simulates *LAI* for Botswana field grown Uniswa Red (N-S, 0.65 to 0.96; MAE, ± 0.08 to 0.14) better than DipC (N-S, 0.43 to 0.93; MAE, ± 0.11 to 0.23) and OM1 (N-S, 0.42 to 0.92; MAE, ± 0.11 to 0.23). *LAI* simulations for OM1 reported that relatively higher deviation from the measured values consistently as in leaf number compared to Uniswa Red and OM1.

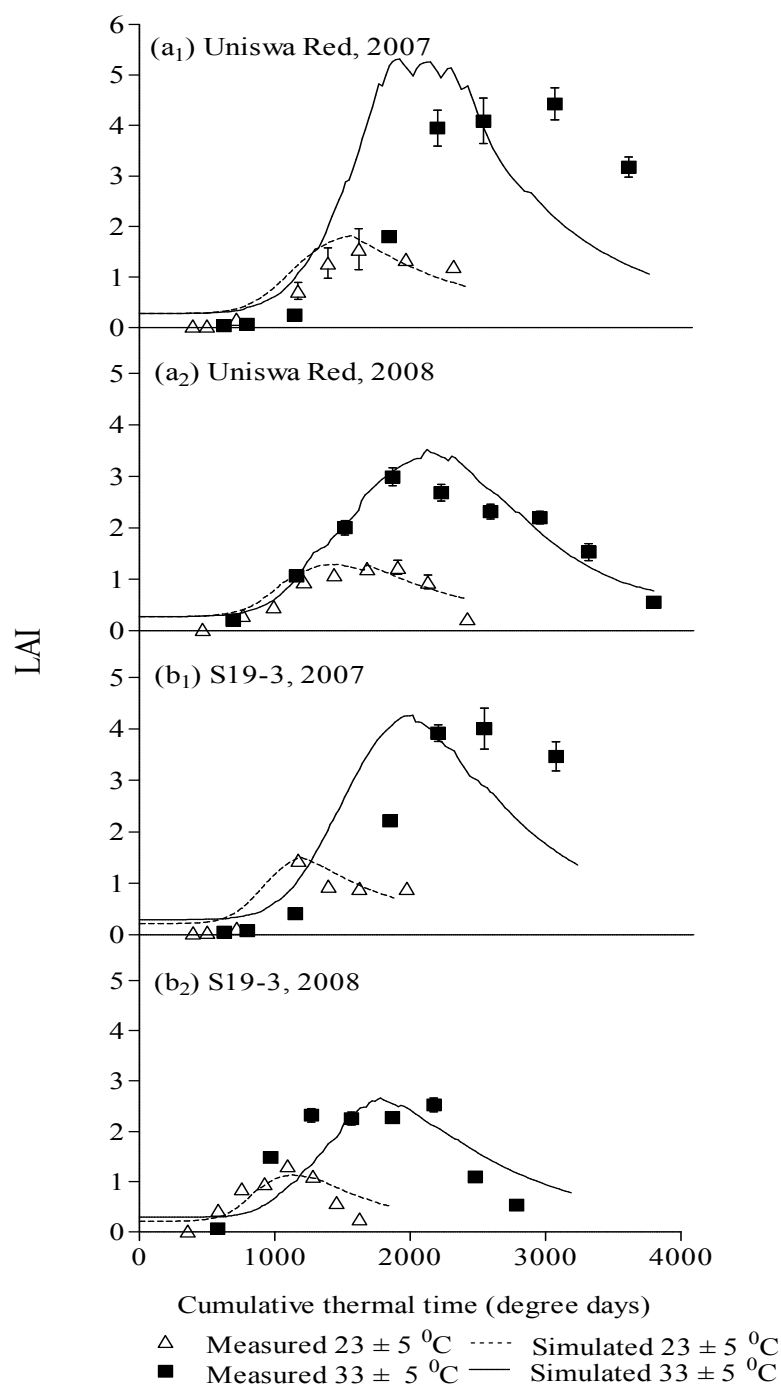


Figure 5. 7. Validation of *LAI* with cumulative thermal time grown under glasshouse conditions for two bambara groundnut landraces Uniswa Red (a₁, a₂), S19-3 (b₁, b₂) with drought at 77 DAS (TCRU 2007 experiment) and 33 DAS (TCRU-2008 experiment) respectively. Measured data are the average of twenty (23 ± 5 °C) and thirty (33 ± 5 °C) plants per landrace. Vertical bars are standard error (\pm SE).

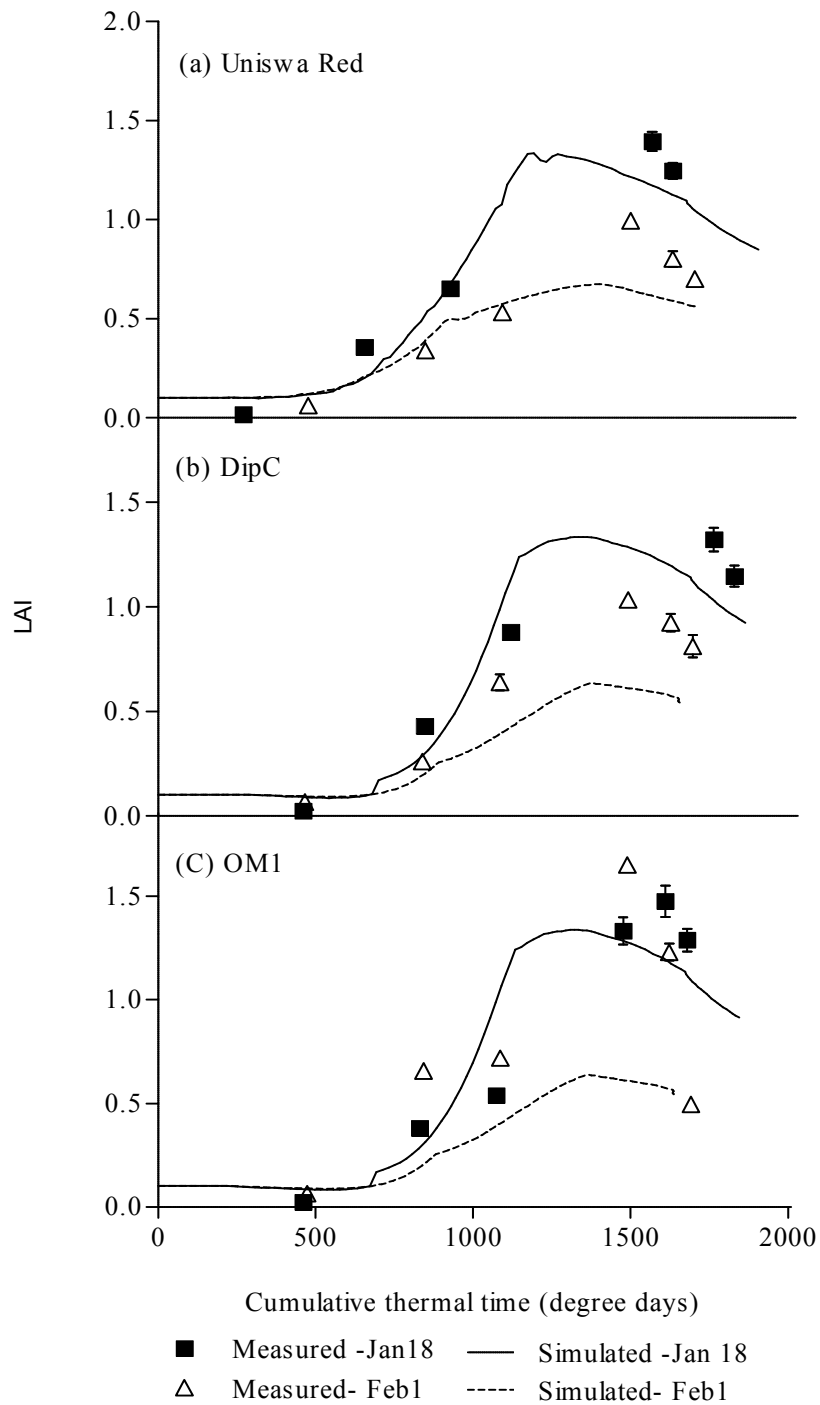


Figure 5. 8. Validation of *LAI* per measured at field sites in Botswana for two sowing dates: January 18 and February 1 in growing season 2006/2007 for three bambara groundnut landraces (a) Uniswa Red (b) DipC (c) OM1. Measured data are the average of six plants per landrace. Vertical bars are standard error (\pm SE).

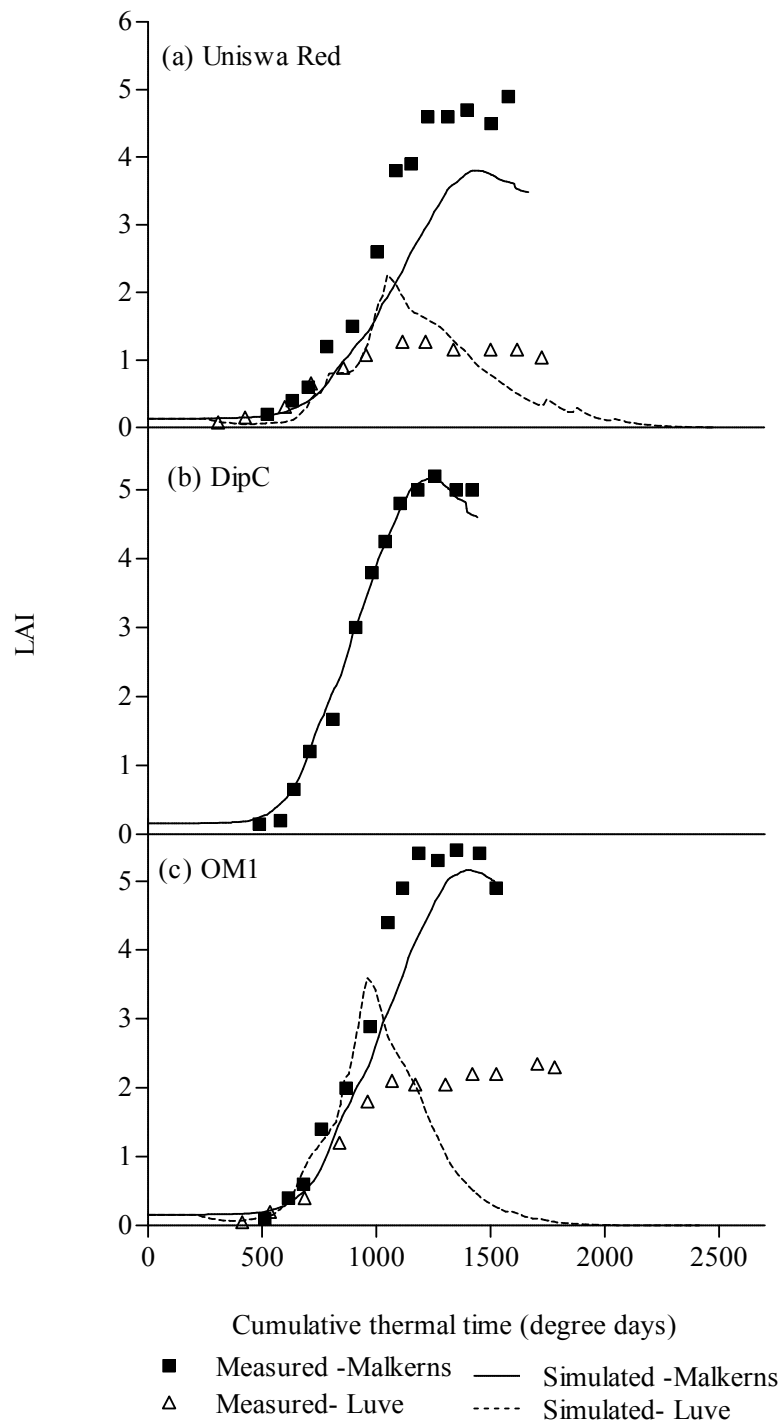


Figure 5. 9. Validation of *LAI* measured at field sites in Swaziland Malkerns and Luve for three landraces for growing season 2002/2003 (a) Uniswa Red (b) DipC (c) OM1. Measured data are the average of ten plants per landrace.

Table 5.3. Comparison of *LAI* model with experimental data for glasshouse (TCRU) and filed experiments in Botswana and Swaziland.

Location/Experiment Treatment	Period	Number of observations	N-S	MAE
TCRU-glasshouse				
Uniswa Red : 23 ± 5 °C	2007	08	0.74	0.28
Uniswa Red : 33 ± 5 °C	2007	08	0.13	1.27
S91-3 : 23 ± 5 °C	2007	08	0.58	0.29
S91-3 : 33 ± 5 °C	2007	08	0.87	0.47
TCRU-glasshouse				
Uniswa Red : 23 ± 5 °C	2008	09	0.73	0.20
Uniswa Red : 33 ± 5 °C	2008	09	0.88	0.24
S91-3 : 23 ± 5 °C	2008	09	0.65	0.21
S91-3 : 33 ± 5 °C	2008	09	0.55	0.50
Botswana				
Uniswa Red : Jan 18	2007	06	0.96	0.08
Uniswa Red : Feb1	2007	06	0.65	0.14
DipC : Jan 18	2007	06	0.93	0.11
DipC : Feb 1	2007	06	0.43	0.23
OM1 : Jan 18	2007	06	0.92	0.11
OM1 : Feb 1	2007	06	0.42	0.23
Swaziland				
Uniswa Red : Malkerns	2002/03	13	0.70	0.82
Uniswa Red : Luve	2002/03	12	0.16	0.30
DipC	2002/03	13	0.99	0.17
OM1 : Malkerns	2002/03	13	0.89	0.53
OM1 : Luve	2002/03	12	-1.32	0.98

BAMGRO was also tested for two field trials in Swaziland (Malkerns and Luve). As explained in Chapter 3, Malkerns reported non- water limited condition during the experimental period (December 2002 to May 2003) whereas the Luve experiment was water limited. The experimental observations reported that *LAI* showed strong reduction with drought stress in Luve (Figure 5.9). For the three landraces (Uniswa Red, DipC and OM1) the model simulation for *LAI* was well correlated with higher N-S (ranges from 0.70 to 0.99) and lower MAE (± 0.17 -0.82) in Malkerns but it showed an under estimation during latter part of the crop cycle for Luve experiment (Figure 5.9). However, BAMGRO is successful in capturing the drought effect in Luve experiment, thus indicating severe reduction in *LAI*.

The BAMGRO model is intended to predict the performance of different genotypes under variable climates. Therefore individual model comparison for *LAI* from glasshouse, field in Botswana (Notwane) and Swaziland (Malkerns and Luve) were pooled for each landrace (Figure 5.10). The statistical comparison of the model for the four tested landraces: S19-3, Uniswa Red, DipC and OM1 are summarised in Table 5.4. Overall, simulated *LAI* correlated well with measured values for all tested landraces (N-S ranges from 0.78 to 0.99) with maximum MAE ± 0.57 . The intercept of the regression line was not significantly ($p > 0.05$) different to the intercept (zero) of 1:1 line and simulations start through the origin. However, the slope of regression line was significantly ($p < 0.05$) different to the slope (one) of 1:1 line except in DipC suggesting an underestimation.

Table 5.4. Comparison of *LAI* model with experimental data for glasshouse (TCRU) and filed experiments in Botswana and Swaziland for landraces S19-3, Uniswa Red, DipC and OM1.

Landrace	Number of observations	N-S	MAE	Slope	Intercept
Uniswa Red	80	0.80	0.41	0.74 ± 0.05	-0.35 ± 0.10
S19-3	34	0.84	0.36	0.82 ± 0.06	-0.27 ± 0.13
DipC	25	0.99	0.14	0.98 ± 0.02	-0.02 ± 0.05
OM1	37	0.78	0.57	0.83 ± 0.06	0.10 ± 0.06

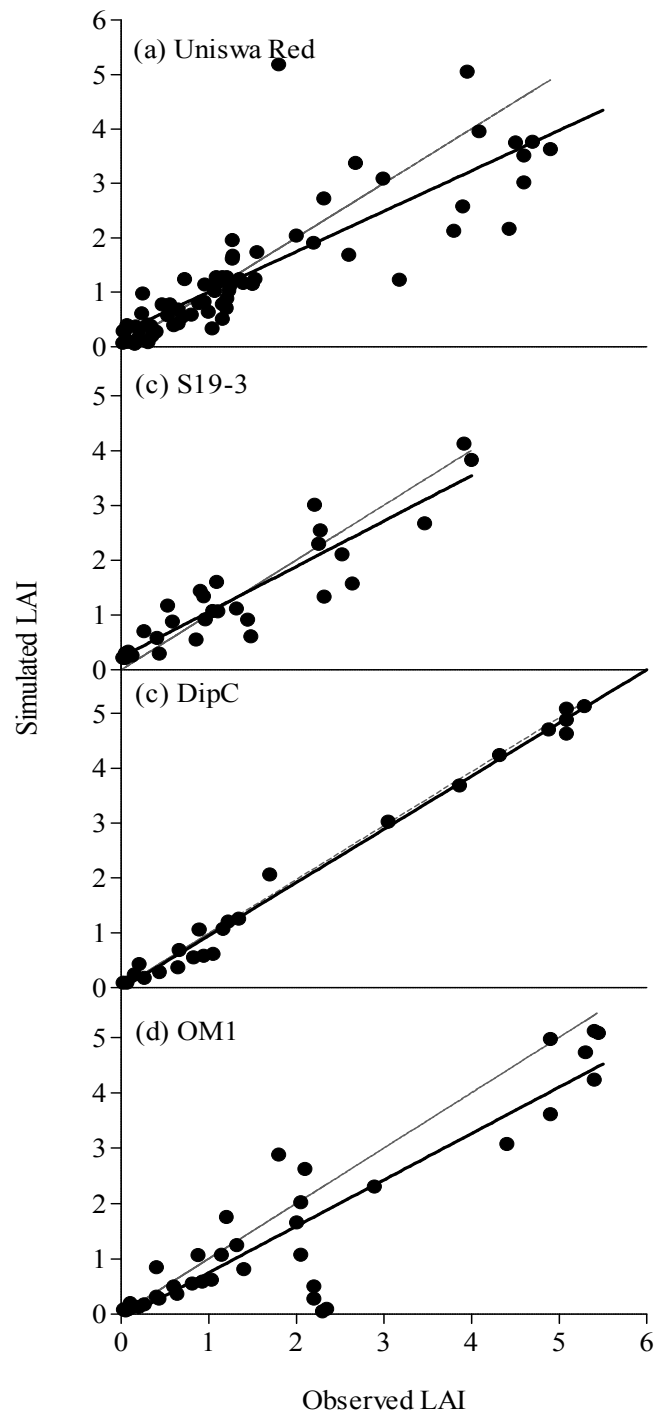


Figure 5.10. Comparison between measured and simulated *LAI* for tested four landraces in glasshouse experiments, Nottingham, UK and field sites in Botswana and Swaziland (a) Uniswa Red (b) S19-3 (c) DipC (d) OM1 1:1 line (---) and regression line (—).

5.4 CHAPTER SUMMARY

- A model for simulation of leaf appearance, leaf area expansion and senescence is developed by this study as a modified approach of previous bambara groundnut models and other classical crop simulation models. The main Eqs. are 5.3, 5.4, 5.14 and 5.16.
- The functions and relationships were derived from the glasshouse experiments Nottingham, UK, University of Copenhagen, Denmark and from published information. The model was validated for glasshouse experiments and field trials in Botswana, and Swaziland.
- The simulation results for leaf number reported strong correlation with observations in glasshouse but over estimation for Uniswa Red (HT) and S19-3 (LT) while it was poor in the Botswana field experiments.
- *LAI* showed a good fit to the experimental data for glasshouse and Swaziland (Malkerns) mainly.
- The combined results of *LAI* for individual landrace are well correlated with 1:1 line but show an underestimation except in DipC.

CHAPTER 6

6.0 MODELLING DRY MATTER PRODUCTION AND YIELD OF BAMBARA GROUNDNUT FOR ABIOTIC STRESS

6.1 INTRODUCTION

Most crop simulation models estimate the daily increase in total dry matter as the product of incident solar radiation ($\text{MJ m}^{-2} \text{ d}^{-1}$), the fractional interception of radiation and efficiency of conversion of intercepted radiation into biomass, i.e. radiation use efficiency (ϵ_s , g MJ^{-1}). The fraction of intercepted radiation is dependent on leaf area index (LAI) and light extinction coefficient (k) (Sinclair, 1986; Hammer et al., 1995; Robertson et al., 2002). The previous bambara groundnut model developed in BAMFOOD project (Cornelissen, 2005) uses an empirical framework to simulate dry matter production and yield considering crop yield to be (a) potential (i.e. limited only by temperature, solar radiation, photoperiod, CO_2 level and genotype, Eq. 6.1), and (b) water-limited. In case of water limitation the dry matter is corrected by a multiplier for water stress (WM_I), which is calculated as the ratio between water supply and potential transpiration. Hence yield is,

$$Yield = \sum_{i=1}^{i=n} S_r \times \epsilon_s \times (1 - \exp^{-k \times LAI}) \times WM_I \times HI \quad 6.1$$

Where,

$Yield$	= the end-of season yield ($\text{kg ha}^{-1} \text{ Y}^{-1}$),
S_r	= short-wave solar radiation over growing period ($\text{MJ m}^{-2} \text{ d}^{-1}$)
ϵ_s	= efficiency of conversion of radiation into biomass (g MJ^{-1})
k	= light extinction coefficient,
LAI	= leaf area index
HI	= harvest index
WM_I	= ratio between water supply and potential transpiration

Considering the components of Eq.6.1 gives an indication of the most important factor determining the biomass production and yield. The incident solar radiation cannot be influenced and will be the same for all plants in the field. Therefore k and ϵ_s are the main coefficients used for simulation of biomass. There is limited information on k and ϵ_s for bambara groundnut.

The subsequent step in modelling dry matter production and yield is to distribute produced biomass to different organs like leaves, stems, roots and pods based on partitioning coefficients (Robertson et al., 2002). Progression through phenological phases causes changes to dry matter partitioning between roots and above ground parts (Robertson et al., 2001). However simulation of dry matter partitioning is one of the weak areas in crop growth models (Marcelis, 1994). Few physiological models have been validated for dry matter partitioning due to the lack of quantitative crop data. Marcelis (1993a) reviewed six main approaches to simulate dry matter partitioning as (1) functional equilibrium (2) transport and sink regulation (3) physical analogue (4) potential demand functions of sinks and (5) potential demands with priority functions. According to Marcelis (1993a), for indeterminate crops such as bambara groundnut potential demand with a priority function for dry matter flow to the reproductive organs during reproductive period is more appropriate.

The previous bambara groundnut models BAMnut and BAMFOOD project model use Specific Leaf Area (SLA) to determine the weight of leaves and thereby, weight increase in each plant component is simulated using constant partitioning coefficients throughout the crop cycle and variable climatic conditions. However the dry matter partitioning during the crop duration under different climatic conditions have to be considered carefully as it will lead to discrepancies in simulations from measured data.

Therefore, the main objectives of current study were to (1) determine ϵ_s and k of bambara groundnut landraces at different air temperatures and limiting and non-limiting soil moisture regimes (2) develop a model for dry matter production (3)

develop functions for dry matter partitioning and (4) simulate yield based on potential demand with priority function for reproductive growth under abiotic stress. The present model BAMGRO uses the framework of previous BAMFOOD project model for dry matter production using k and ϵ_s as a starting point. Dry matter partitioning among the organs in the plant is simulated based on the phenological stage and drought stress.

Model development is described in section 6.2 together with suitable dry matter production and yield data and parameterisation results. This is followed by model validation results (section 6.3) and Chapter summary (section 6.4).

6.2 MODEL DEVELOPMENT AND PARAMETERISATION

6.2.1 Dry Matter Production

The model calculates potential daily crop dry matter production rate from LAI , k and ϵ_s by integration of leaf assimilation rates over total crop canopy. Photosynthetic characteristics of individual leaves are assumed to be identical. The daily rate of potential dry matter assimilation (potential growth) is calculated according to Eq. 6.2 as a modified approach of starting framework (Eq. 6.1) in previous BAMFOOD project model.

$$LLG = PAR_{frac} \times S_i \times \epsilon_s \times (1 - \exp^{-k \times LAI}) \quad 6.2$$

Where,

LLG = light limited growth ($\text{g m}^{-2} \text{d}^{-1}$)

S_i = short wave solar radiation ($\text{MJ m}^{-2} \text{d}^{-1}$)

ϵ_s = efficiency of conversion of this solar radiation (g MJ^{-1})

LAI = leaf area index (Eq. 5.16)

PAR_{frac} = fraction of Photosynthetically Active Radiation (50% of S_i)

LLG is only restricted by light (S_i) and actual daily increase in growth (G_{actual}) is calculated from the minimum of two potential growth rates (Eq. 6.3), one

determined by intercepted radiation (Light Limited Growth-*LLG*, Eq.6.2) and the other by soil water supply (Water Limited Growth-*WLG*, Eq. 7.6). Simply *WLG* (Chapter 7) is calculated by the water productivity function, using potential water uptake by roots and transpiration equivalent that is normalised for variable temperatures and humidity levels using saturation deficit values (Chapter 7; Eq. 7.6).

$$G_{actual} = \min(LLG, WLG) \quad 6.3$$

For light attenuation through the canopy, Beer's Law (Goudriaan & Monteith, 1990) gives the fraction f of incident radiation intercepted by foliage.

$$f = 1 - \exp^{(-k \times LAI)} \quad 6.4$$

Where,

k = light extinction coefficient

Light extinction coefficient (k) was determined by Eq. 6.4 using the data of fractional interception (f) and LAI (Eq. 5.16) from glasshouse experiments (TCRU-2006). The light extinction coefficient (k) through the crop stands in different treatments were calculated as the slope of the regression of $\ln(1-f)$ on LAI . According to TCRU experiment 2006, k is common for all the landraces under two temperature conditions: HT (33 ± 5 °C) and LT (23 ± 5 °C) with a value of 0.6 ± 0.057 (Table 6.1). The cumulative total solar radiation interception was calculated as the product of daily incoming solar radiation and f for each day after sowing. When total dry matter (TDM) at different growth stages was regressed against cumulative intercepted solar radiation (S_i), the slope is a measure of ϵ_s ($g\ MJ^{-1}$). The measured data from glasshouse experiment (TCRU-2006), University of

Nottingham, UK were used to estimate the ϵ_s (Figure 6.1). The slopes of the regression lines explain numerical value for ϵ_s for each landrace under two temperature conditions; LT and HT. There were no significant differences ($p > 0.05$) between landraces in low temperature treatments (0.69 g MJ^{-1} and 0.70 g MJ^{-1}). However, a significant difference ($p < 0.01$) was found between high temperature treatments (1.03 g MJ^{-1} and 1.55 g MJ^{-1}). These regressions showed that low temperature reduced the mean ϵ_s from 1.55 g MJ^{-1} and 1.03 g MJ^{-1} in S19-3 and Uniswa Red respectively to 0.7 g MJ^{-1} (Figure 6.1). BAMGRO model uses ϵ_s values at HT for two landraces Uniswa Red and S19-3 in sub file landrace coefficients and computes the reduction under LT (section 4.3.1).

The results from glasshouse experiment (TCRU-2006) reported that the values of f initially increased rapidly and after which remained stable and finally declined for the two temperature levels (LT, $23 \pm 5^\circ\text{C}$ and HT, $33 \pm 5^\circ\text{C}$) and two landraces (Uniswa Red and S19-3). For tested two landraces, HT ($33 \pm 5^\circ\text{C}$) treatments recorded higher f than LT. The maximum f values for two landraces were close to 0.90 and minimum ranges around 0.75. The difference between LT and HT was higher in Uniswa Red (0.15) compared to S19-3 (0.10).

These values of k (0.60 ± 0.057) and ϵ_s for two landraces (Uniswa Red and S19-3) were used to simulate dry matter production in bambara groundnut landraces using Eq. 6.2 when there is no water limitation and calibration results for total dry matter production (TDM) for glasshouse experiment 2006 (TCRU-2006) are shown in Figure 6.2. The behaviour of the dry matter production function in BAMGRO model was tested with temperature stress switch off ($TSTRESS=1$) and simulation results under LT and HT are presented in Figure 6.2.

Table 6.1. Mean light extinction coefficient values (k) for two landraces Uniswa Red and S19-3.

Landrace	$k \pm \text{SE}$
Uniswa Red	0.60 ± 0.052
S19-3	0.61 ± 0.063
Mean	0.60 ± 0.057

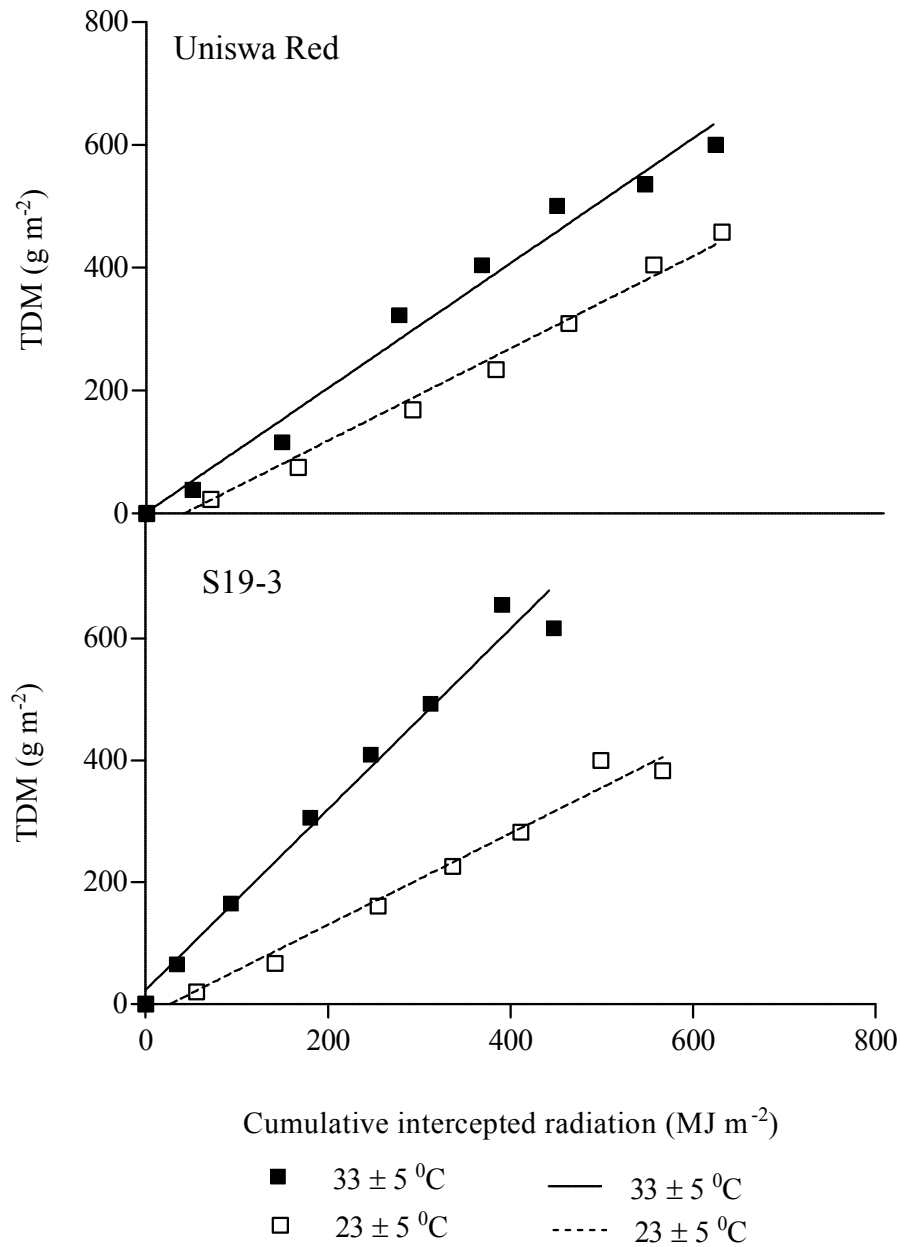


Figure 6.1. Regression analysis of total dry matter (g m^{-2}) against cumulative intercepted radiation (MJ m^{-2}) for two bambara groundnut landraces grown under high temperature (closed symbols) and low temperature (open symbols) conditions in glasshouses: Regression equations are: For Uniswa Red, low temperature ($23 \pm 5 ^\circ\text{C}$) and high temperature ($33 \pm 5 ^\circ\text{C}$), $Y = 0.69x$; $r^2 = 0.97$, $Y = 1.03x$; $r^2 = 0.98$, and for S19-3, $Y = 0.70x$; $r^2 = 0.97$, $Y = 1.55x$; $r^2 = 0.97$, respectively.

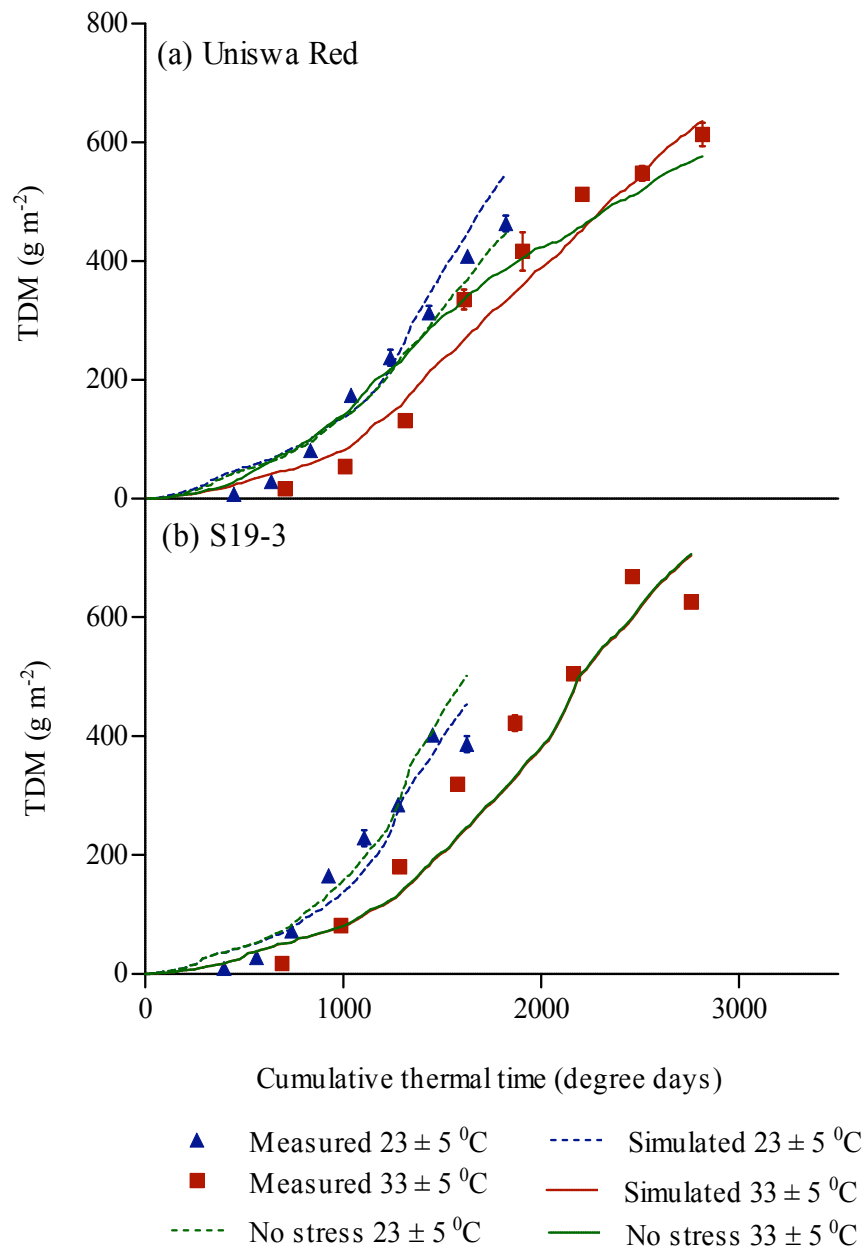


Figure 6.2. Model calibration results for total dry matter production with cumulative thermal time in landraces, Uniswa Red (a) and S19-3 (b) grown at low temperature (23 ± 5 °C) and high temperature (33 ± 5 °C): TCRU glasshouse experiment 2006. Measured data are the average of twenty (23 ± 5 °C) and thirty (33 ± 5 °C) plants per landrace. The simulation results with no stress ($TSRESS=1$) are shown with calibration results for LT and HT. Vertical bars are standard error (\pm SE). Simulated lines were obtained using Eq. 6.3 with parameters and correlation coefficients in Table 6.1.

6.2.2 Crop Phenology

The development of bambara groundnut can be explained in terms of vegetative (germination, emergence, vegetative) and reproductive (flowering and pod formation) phases. Unlike cereals, there is an overlapping of these two phases, as leaf production continues after flowering and podding. There is a phenological switch, which is operated between the vegetative and reproductive phases.

The progression through phenological phases signals changes in the growth and partitioning of biomass to leaves, stems, roots and pods depending on the stage of growth. Phenology is simulated from sowing through 5 stages (1) emerging, (2) vegetative phase, (3) flowering, (4) pod filling, (5) maturity. Germination is set to occur on the day after sowing in all landraces. Each of the phases in the phenology of the crop is assumed to require a specific number of phenochrons (Eq. 6.5) before it is completed and enters the next phase.

Table 6.2. Description of growth stages.

Stage	Description
Emerging	From sowing until first full leaf above the ground
Vegetative	Start at the end of emerging until maturity
Flowering	Start at 50% of the crop in flower until maturity (indeterminate)
Pod filling	Start determined by the start of first podding
Maturing	Last phase, end of vegetative phase, crop is senescing

(Cornelissen, 2005)

A phenochron is defined as the advancement in the phenological age of the crop over growing period when temperature and photoperiod are at their optimum values (Matthews and Stephens, 1998a). Thus the advancement of phenological age (Ad , phenochrons) of the crop on day n (days since sowing) is given by Eq.6.5.

$$\frac{dAd}{dt} = \sum_{i=1}^{i=n} \frac{\Delta(TT)}{(T_{opt} - T_{base})} \times f(\theta_{d(i)}) \quad 6.5$$

Where,

A_d = Phenochrons

n = number of days experienced by the crop since sowing

$f(\theta_{d(i)})$ = function relating to photoperiod (Matthews and Stephens, 1998)

The function related to photoperiod is considered to be constant when daylength is below 12 h and linear reduction is hypothesized between 12 h and 18 h (Cornelissen, 2005). The effect of photoperiod on phenology through $f(\theta_{d(i)})$ directly responds to the delay in pod filling when the crop is grown above 12 h daylength (Figure 6.3). DL_{fac} (Eq. 4.7) which explains the effect of photoperiod with a positive linear relationship on rate of new leaf production is used to estimate the multiplier (Figure 6.3). According to the experimental observations, the inversely proportionate relationship between leaf number and pod number explains the delay in pod formation during the photoperiod above 12 h. Therefore BAMGRO simply assumes, $f(\theta_{d(i)})$ is inversely proportional to DL_{fac} (Eq. 6.3).

$$f\theta_{d(i)} = \frac{1}{DL_{fac}} \quad 6.6$$

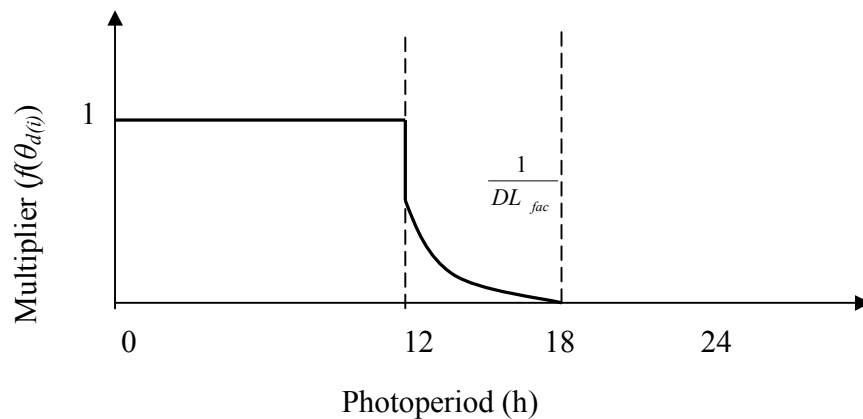


Figure 6.3. Function relating daily photoperiod to a multiplier.

The number of phenochrons for each growth stage was calculated from previous TCRU experimental data and published information (Table 6.2). The base temperature and the upper limit for germination of bambara groundnut landraces have been identified as 10 °C and 42 °C respectively. According to Massawe et al., (2003) base temperature for germination varies across landraces from 8-12 °C. However, considering the agro-ecological adaptations of Uniswa Red and S19-3 and experimental evidences of glasshouse (TCRU-2006) experiment, the present model adjusts these values of the cardinal temperatures (Table 6.3).

Table 6.3. Landrace specific cardinal temperatures used for the calculation of phenochrons and predetermined number of phenochrons for each phenological stage for two landraces: Uniswa Red and S19-3 (TCRU glasshouse experiment, 2002 and 2006).

Landrace coefficient	Description	Cardinal temperatures	
		Uniswa Red	S19-3
T_{base}	Base temperature	8.5	12
T_{opt}	Optimum temperature	28	30
T_{high}	Ceiling temperature	38	45
		Number of Phenochrons	
		Uniswa Red	S19-3
P_0	Phenological time from sowing to emergence	6	10
P_1	Phenological time from emergence to end of juvenile phase	22	18
P_2	Phenological duration of the inductive period	22	23
P_3	Phenological time from emergence to flowering	35	25
P_4	Phenological time from flowering to podding	20	16
P_5	Phenological time for pod maturity	43	39
P_6	Phenological duration from maturity to harvest	3	1

6.2.3 Dry Matter Partitioning

As described below daily growth is the net result of assimilates initially relocated from seeds during germination, net photosynthesis and losses through leaf senescence. Biomass partitioning is computed according to the approach of CROPGRO (Boote et al., 2002a). Dry matter partitioning is divided into 3 main phases: germination to emergence, vegetative to inductive and flowering to maturity. The present model BAMGRO develops new functions and relationships to simulate dry matter partition depending on the stage of growth.

Germination to emergence

During germination, assimilates stored in seeds are mobilized and relocated from the seed for the initial growth of roots in young seedlings. The relocation rate is a constant and BAMGRO calculates relocation in g m^{-2} , using the individual seed weight and population density (plants m^{-2}) according to Eq. 6.7.

$$\frac{d\text{Seedreloc}}{dt} = \text{Density} \times \text{SeedW} \times \text{Frs} \quad 6.7$$

Where,

Seedreloc = daily relocation of assimilates from seed (g m^{-2})

SeedW = individual grain weight (g seed^{-1})

Frs = recoverable fraction of assimilates per day

The weight of seed (*SeedW*) is considered as uniform between landraces and it is 0.6 g whereas the daily fraction of partitioning to roots (*Frs*) is 0.02.

Vegetative to Inductive

Dry matter (G_{actual}) partitioning allocates the largest proportion to the above ground parts (leaves and stems) during vegetative growth. At the end of each simulated day, remaining biomass is directed towards roots based on the requirement of the roots that is adjusted according to growth phase and stress condition.

$$Total = F_Leaf + F_Stem + F_Root = 1 \quad 6.8$$

Where,

$Total$ = daily sum of partitioning fractions (1)

F_Leaf = fraction of leaf

F_Stem = fraction of stem

F_Root = fraction of roots

According to the TCRU experimental data of 2006 (Figure 6.4), almost all the landraces have initial value for leaf fraction (0.70 ± 0.028) which decreased with the accumulation of thermal units and further altered according to the level of drought stress ($WSTRESS$) and temperature stress. In the later case calibration results reported that F_Leaf is decreased in LT at a higher rate compared to HT corresponding greater increase in F_Pod in LT (Figure 6.4).

$$F_Leaf = (0.70 - 0.00003 \times TT) \times Ks_3 \quad \text{for } T_{mean} > T_{opt} \quad 6.9$$

$$F_Leaf = (0.70 - 0.0001 \times TT) \times Ks_3 \quad \text{for } T_{mean} \leq T_{opt} \quad 6.10$$

Where,

Ks_3 = $WSTRESS$ (Eq. 4.4)

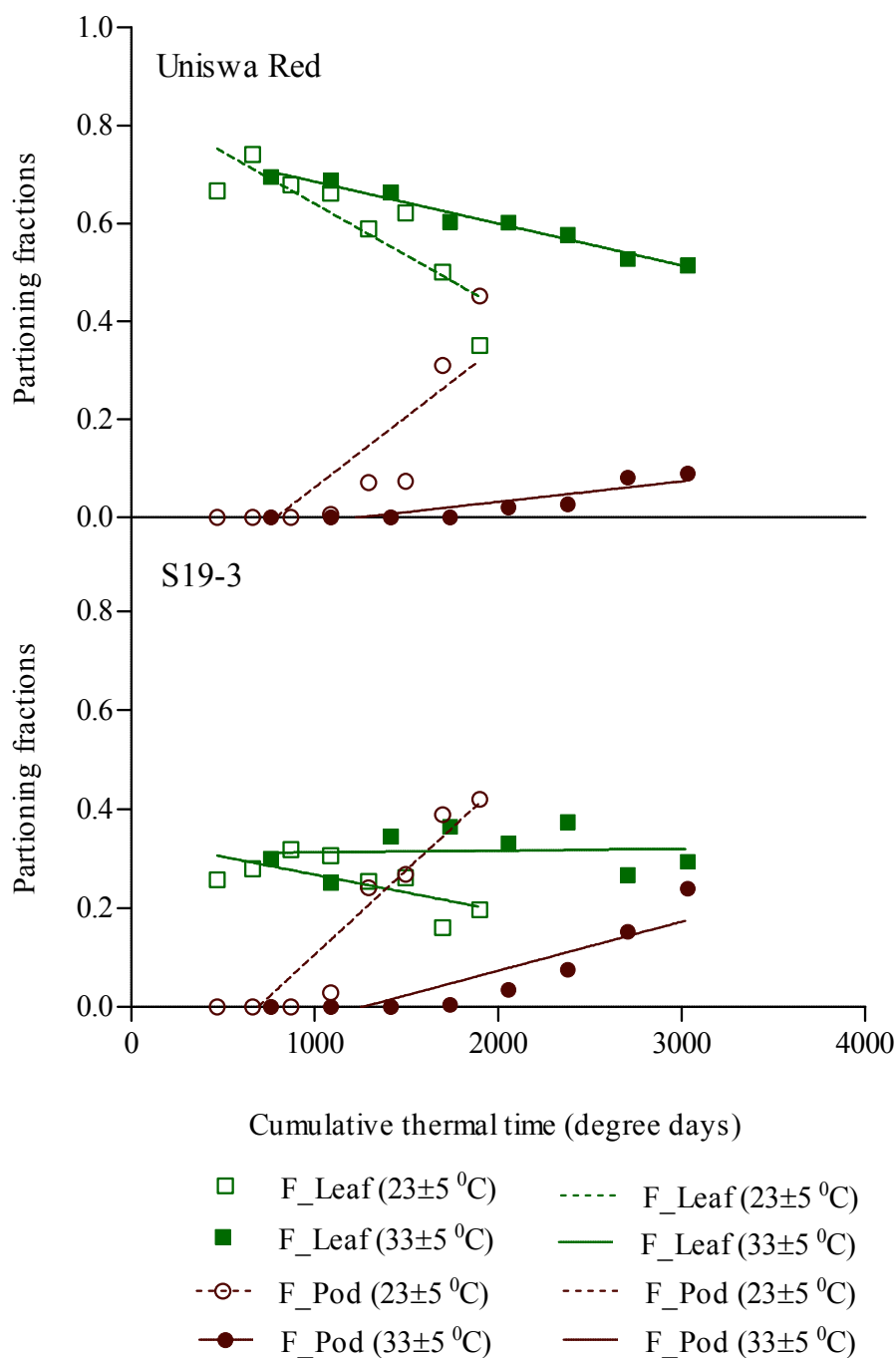


Figure 6.4. Variation of partitioning fractions of leaves and pods with cumulative thermal time in landraces, Uniswa Red (a) and S19-3 (b) grown at low temperature ($23 \pm 5^{\circ}\text{C}$) and high temperature ($33 \pm 5^{\circ}\text{C}$): TCRU glasshouse experiment 2006. Measured data are the average of twenty ($23 \pm 5^{\circ}\text{C}$) and thirty ($33 \pm 5^{\circ}\text{C}$) plants per landrace.

Partitioning to stem showed fairly a constant value (Eq. 6.11) throughout the vegetative phase and experimental data revealed this value as (0.26 ± 0.014) for the tested two landraces (Uniswa Red and S19-3) (Figure 6.4).

$$F_Stem = 0.26 \quad 6.11$$

After allocation of dry matter to leaves and stems, any remaining is partitioned to roots (Eq. 6.11).

$$F_Root = Total - (F_Stem + F_Leaf) \quad 6.12$$

These partitioning coefficients are used to determine the increase in leaf weight, dead leaf weight, stem weight and root weight considering total dry matter produced (G_{actual}) in Eq. 6.3 and senescence fraction Ks_2 (Chapter 5: Eq. 5.13).

$$\frac{dLW}{dt} = (G_{actual} \times F_Leaf) - \left(\frac{dDEADLW}{dt} \right) \quad 6.13$$

$$\frac{dDEADLW}{dt} = LW \times Ks_2 \quad 6.14$$

$$\frac{dSTEMW}{dt} = G_{actual} \times F_Stem \quad 6.15$$

Where,

LW = leaf weight ($g\ m^{-2}$)

$DEADLW$ = dead leaf weight ($g\ m^{-2}$)

$STEMW$ = stem weight ($g\ m^{-2}$)

However until emergence the root growth is dependent on biomass mobilized from seeds (*Seedreloc*) and thereafter daily dry matter produced (G_{actual}) is partitioned to roots depending on the fraction of root.

$$\frac{dRW}{dt} = Seedreloc + (G_{actual} \times F_Root) \quad 6.16$$

Where,

RW = root weight (g m^{-2})

Flowering to maturity

The stem weight remains fairly constant during the reproductive phase giving priority to reproductive organs. Being an indeterminate crop bambara groundnut continues leaf production until harvesting but at a lower rate after floral initiation compared to the vegetative stage. Even though fractional partitioning to leaves continues during the flowering stage, flower and pod formation are the leading processes during this period (i.e. priority demand function; Marcelis (1993a)). During the reproductive phase of the crop, total of fractions consisted of leaf, stem, root and pod.

The fractional partitioning to leaf and stem are similar to vegetative phase and calculated according to Eqs. 6.9, 6.10 and 6.11. However the root fraction is reduced to a constant ratio between shoots and roots according to the experimental results of TCRU-2003. Mwale (2005) reported a significant reduction in root growth during reproductive phase. Since limited information is available on BAMGRO simply uses a constant value of 0.04 as root: shoot ratio (Eq. 6.17).

$$F_Root = (F_Leaf + F_Stem) \times 0.04 \quad 6.17$$

6.2.4 Yield Formation

The fractional partition to pods is

$$F_Pod = Total - (F_Leaf + F_Stem + F_Root) \quad 6.18$$

Pod formation and pod filling are considered as two independent processes during the reproductive phase. According to the TCRU experiment 2006, the rate of pod formation is inversely proportional to the rate of leaf production and a switch is operated within the model to initiate pods when the rate of leaf production is at its maximum value (Figure 5.1) which is usually coincided with pod initiation. BAMGRO regulates the daily increase in pod number (PN) with accumulation of thermal time up to the maximum value of each landrace (Eq.6.19).

$$\frac{dPN}{dt} = \left(\frac{1}{(LN)} \right) \times \Delta TT \quad 6.19$$

Where,

PN = pod number (plant^{-1})

The weight of individual pod is calculated according to Eq. 6.20 assuming dry matter (G_{actual}) is partitioned to all the pods within the plant uniformly. If the rate of pod filling exceeds the maximum pod filling rate which is assigned to the model it automatically lowers the rate to maintain the maximum size of individual pod. Since dry matter produced is distributed among the pods per unit area, pod number per unit area is calculated using plant density.

$$\frac{dPW}{dt} = \frac{(G_{actual} \times F_Pod)}{(PN \times density)} \quad 6.20$$

Where,

PW = weight of individual pod (g pod^{-1})

However, the maximum number of pods per plant and the size of the individual pod (PW) are controlled with in BAMGRO with user defined maximum values. Based on experimental observations (Cornelissen, 2005), maximum pod number is restricted to 56 ± 15 and 62 ± 25 per plant for Uniswa Red and S19-3 respectively under non limiting moisture and optimum temperatures while the maximum size of a pod is set as 0.35 g. Therefore, the final yield is a product of actual number of pods produced and their individual weight and is calculated according to Eq. 6.21

$$Yield = PW \times PN \times density \quad 6.21$$

Where,

$$Yield = \text{Pod yield (g m}^{-2}\text{)}$$

The model was tested under glasshouse condition to determine the applicability of values used in the function of pod yield and the calibration results from glasshouse experiment 2006 (TCRU-2006) for pod weight is shown in Figure 6.5.

The accuracy and proper functioning of BAMGO model for yield formation under temperature stress was tested with temperature stress function switch off ($TSRESS=1$, Eq. 4.5 and 4.6) and simulation results are shown in Figure 6.5. Swaziland landrace Uniswa Red explains the lower yield under LT and higher in HT when $TSTRESS=1$ (no heat/cold stress) compared to the $TSTRESS$ is switched on. This behaviour of BAMGRO shows the sensitivity of Swaziland landrace, Uniswa Red for temperature stress. Whereas in Namibian landrace, S19-3, there is no noticeably change in yield when $TSRESS$ function is switched off. According to Figure 6.5, S19-3 is not sensitive to $TSTRESS$ function for yield formation. The results clearly show the performance of BAMGRO model for yield under temperature stress.

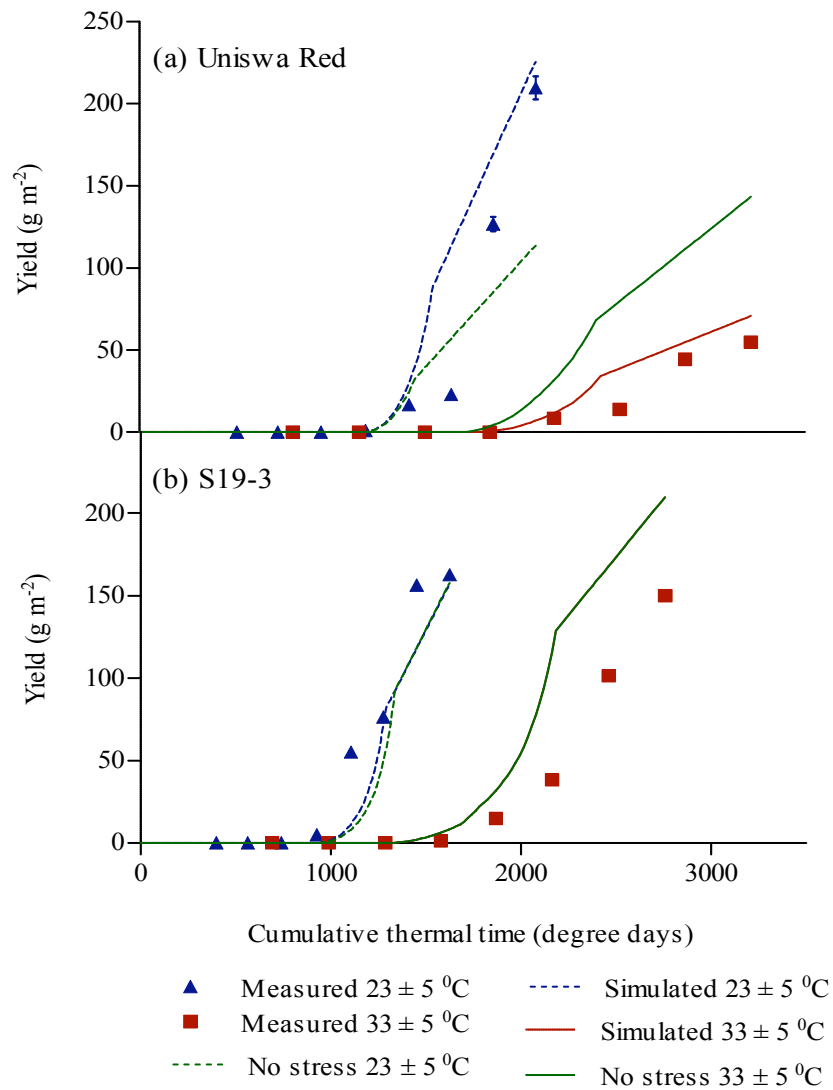


Figure 6.5. Model calibration for yield with cumulative thermal time in landraces, Uniswa Red (a) and S19-3 (b) grown at low temperature (23 ± 5 °C) and high temperature (33 ± 5 °C): TCRU glasshouse experiment 2006. Measured data are the average of twenty (23 ± 5 °C) and thirty (33 ± 5 °C) plants per landrace. The simulation results with no stress ($TSRESS=1$) are shown with calibration results for LT and HT. Vertical bars are standard error (\pm SE). Simulated lines were obtained using Eq. 6.21 with parameters and correlation coefficients specific to each landrace.

6.3 MODEL VALIDATION

6.2.5 Dry Matter Production

According to the experimental results from present study and previous work (Mwale, 2005; Collinson et al., 1996, 1997) G_{actual} (TDM) reduced with drought stress, and varied with changes in daily mean temperature (T_{mean}). Under glasshouse conditions in Nottingham both landraces (Uniswa Red and S19-3), TDM increased with increasing temperature (33 ± 5 °C) exhibiting higher biomass production under HT and reduced in LT (23 ± 5 °C). BAMGRO is successful in explaining the trends due to abiotic stress in simulations of TDM (TCRU: Figure 6.6; Botswana: Figure 6.7; Swaziland: Figure 6.8). The results of model comparison with measured values for N-S and MAE are summarised in Table 6.4.

Two years of glasshouse experiments (TCRU 2007 and 2008) combined two extremes of temperatures with drought stress. The simulation of TDM is mainly under WLG . The model predictions of TDM in Uniswa Red reported a fairly good correlation with N-S of 0.49 and 0.67 under HT in 2007 and 2008 respectively. HT treatment of S19-3 showed relatively lower N-S as 0.61 and 0.30 for 2007 and 2008 seasons respectively with MAE above 100 g m^{-2} . Generally, simulation results of TDM under LT are overestimated for both landraces in 2007 and 2008 thus reporting poor correlation with measured values (N-S ranges from -0.74 to -7.88).

TDM varied with sowing dates and the model simulates the effect of variable climatic conditions in Botswana (Figure 6.7). The plants grown in February 1 and January 18 in the 2007 experiment reported a higher correlation with observed values (N-S, 0.86 to 0.88) and lower MAE (± 16.49 to 35.31 g m^{-2}) for Uniswa Red. The model comparison with measured values of TDM for field grown DipC reported a statistically acceptable results (N-S, 0.72 to 0.81 and MAE, ± 22.6 to 56.30 g m^{-2}) for two sowing dates. OM1 reported relatively lower goodness of fit to the model (N-S, 0.21 to 0.79 and MAE, ± 39.98 to 60.79 g m^{-2}). The model

simulations explains the general trend of *TDM* during the growth cycle for two sowing dates which shows good agreement with measured values at early stages with deviations towards the crop maturity.

BAMGRO was finally tested for two field trials in Swaziland (Malkerns and Luve). As per experimental details explained in Chapter 3, Malkerns and Luve represented irrigated and drought conditions respectively. The correlation of *TDM* simulation with measured values was acceptable for Unswa Red (N-S, 0.66) DipC (N-S, 0.76) and OM1 (N-S, 0.77) for Malkerns field experiments. Although it was poorly simulated under drought stress in Luve for Uniswa Red with lower N-S, 0.12 and higher MAE $\pm 104 \text{ g m}^{-2}$ (Table 6.5), the model prediction for OM1 is well correlated (N-S, 0.81).

Table 6.4. Comparison of *TDM* model with experimental data for glasshouse (TCRU) and filed experiments in Botswana and Swaziland.

Location/Experiment Treatment	Period	Number of observations	N-S	MAE
TCRU-glasshouse				
Uniswa Red: 23 ± 5 °C	2007	08	-7.89	127.98
Uniswa Red: 33 ± 5 °C	2007	08	0.49	115.03
S91-3 : 23 ± 5 °C	2007	08	-0.89	108.14
S91-3 : 33 ± 5 °C	2007	08	0.61	113.22
TCRU-glasshouse				
Uniswa Red: 23 ± 5 °C	2008	09	0.16	70.18
Uniswa Red: 33 ± 5 °C	2008	09	0.67	69.22
S91-3 : 23 ± 5 °C	2008	09	-0.74	95.93
S91-3 : 33 ± 5 °C	2008	09	0.30	112.87
Botswana				
Uniswa Red: Jan 18	2007	06	0.88	35.31
Uniswa Red: Feb1	2007	06	0.86	16.49
DipC : Jan 18	2007	06	0.72	56.30
DipC : Feb 1	2007	06	0.81	22.69
OM1 : Jan 18	2007	06	0.79	39.98
OM1 : Feb 1	2007	06	0.21	60.79
Swaziland				
Uniswa Red: Malkerns	2002/03	13	0.66	64.71
Uniswa Red: Luve	2002/03	12	0.12	104.48
DipC : Malkerns	2002/03	13	0.76	64.25
OM1 : Malkerns	2002/03	13	0.77	67.39
OM1 : Luve	2002/03	12	0.81	49.38

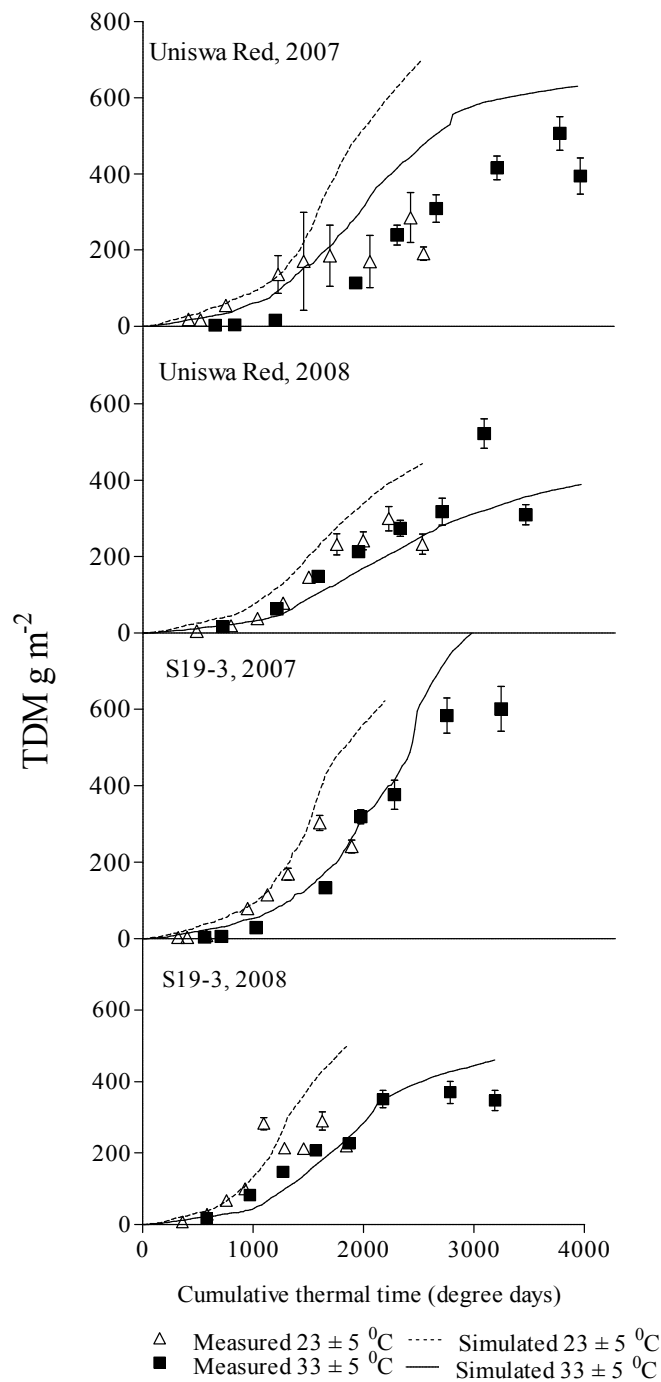


Figure 6. 6. Validation of TDM ($g\ m^{-2}$) with cumulative thermal time grown under glasshouse conditions for two bambara groundnut landraces Uniswa Red (a₁, a₂), S19-3 (b₁, b₂) with drought at 77 (TCRU 2007 experiment) and 33 (TCRU-2008 experiment) respectively. Measured data are the average of twenty ($23 \pm 5\ ^\circ C$) and thirty ($33 \pm 5\ ^\circ C$) plants per landrace. Vertical bars are standard error (\pm SE).

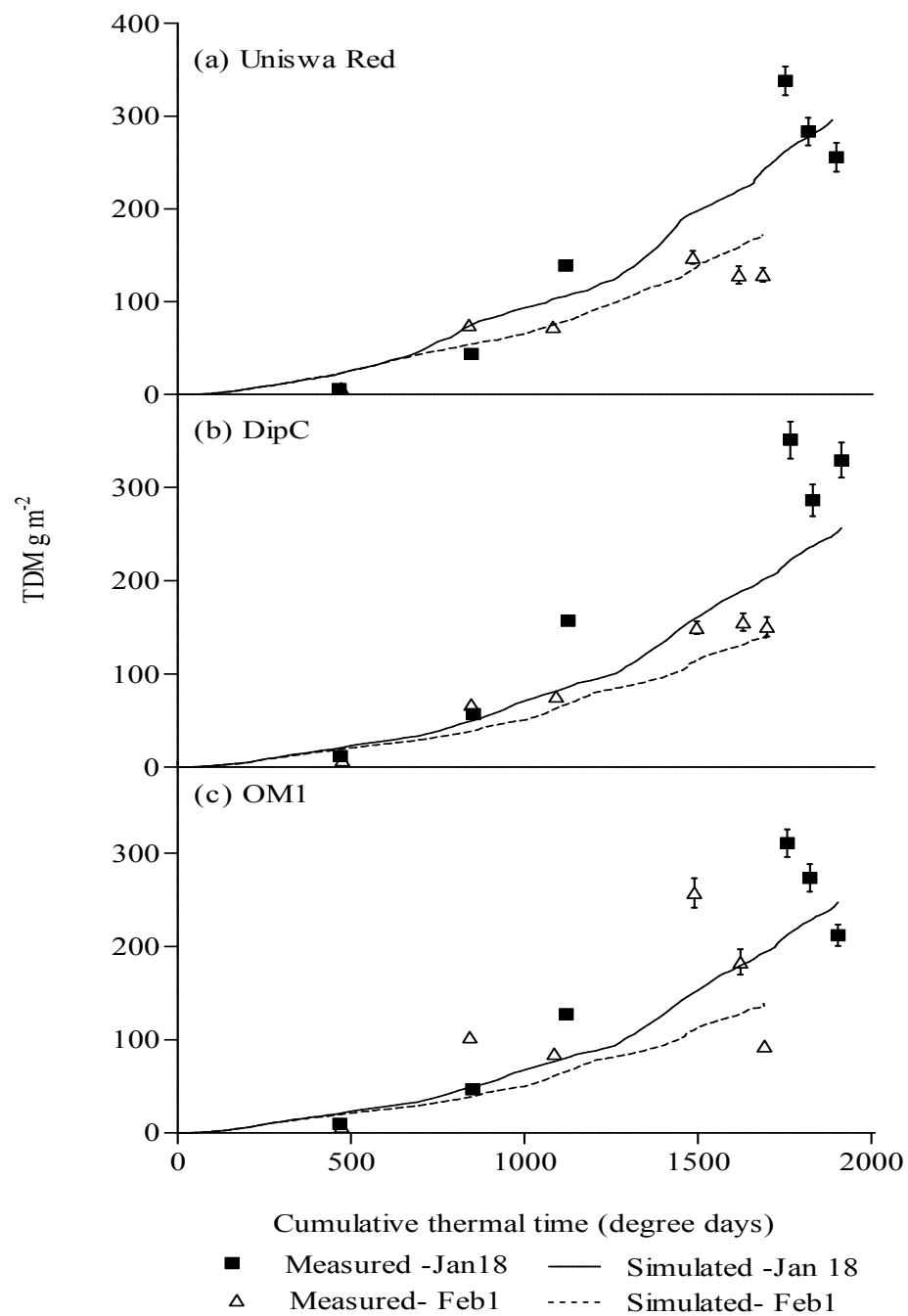


Figure 6. 7. Validation of TDM (g m⁻²) measured at field sites in Botswana for two sowing dates: January 18 and February 1 in growing season 2006/2007 for three bambara groundnut landraces (a) Uniswa Red (b) DipC (c) OM1. Measured data are the average of six plants per landrace. Vertical bars are standard error (\pm SE).

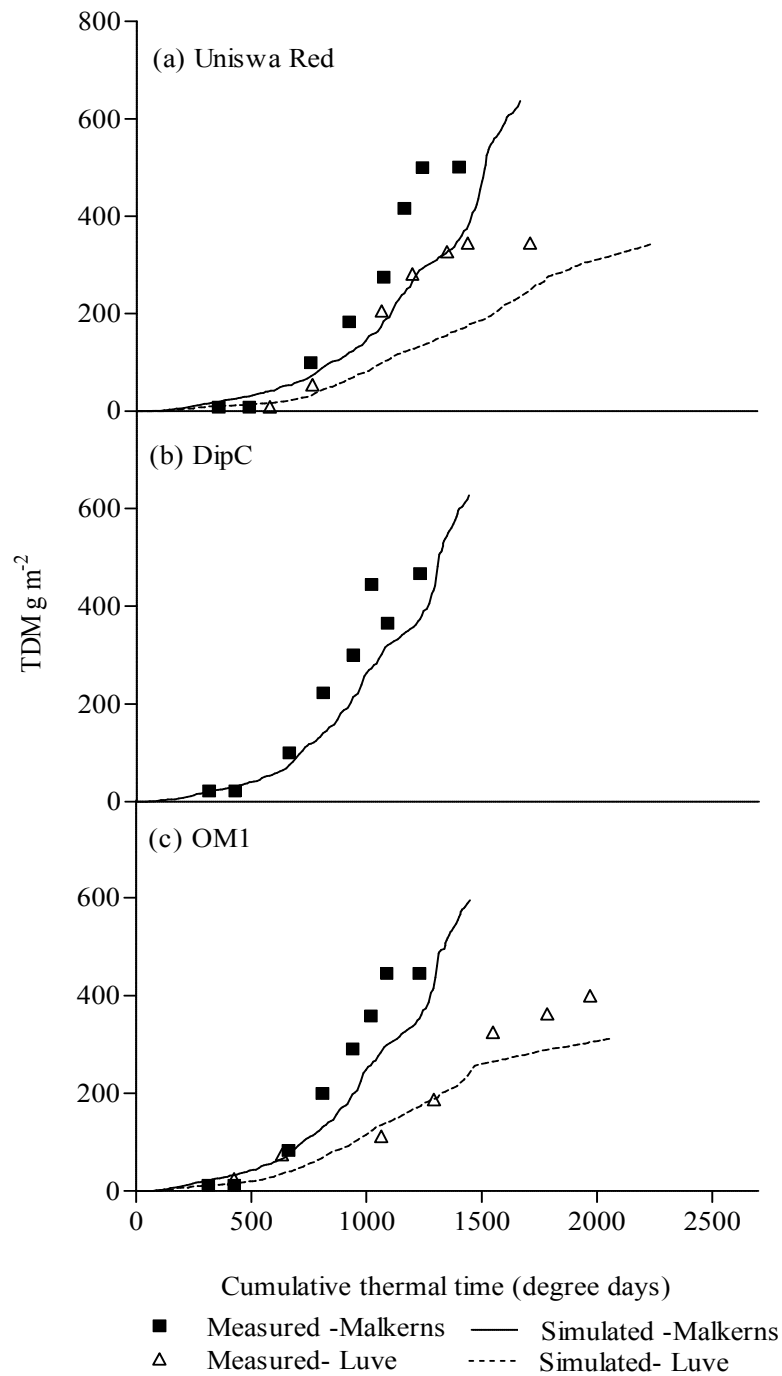


Figure 6.8. Validation of TDM (g m^{-2}) measured at field sites in Swaziland Malkerns and Luve for three landraces for growing season 2002/2003 (a) Uniswa Red (b) DipC (c) OM1. Measured data are the average of ten plants per landrace.

The statistical comparison of the model for the four tested landraces: Uniswa Red, S19-3, DipC and OM1 are summarized in Table 6.5. Overall, simulated *TDM* correlated well with measured values for all tested landraces when it was compared with combined data sets from all the experiments corresponding to each landrace. According to the results from statistical analysis, simulation of biomass production is well correlated with the line of identity (N-S) and MAE ranges from 48.8 to 100 g m⁻² (Table 6.5). However, the slope of the regression line is significantly ($p < 0.05$) lower values (0.71-0.81) compared to the slope (one) of 1:1 line indicating under estimation of the dry matter production (Figure 6.9). The intercept of the regression line was not significantly different ($p > 0.05$) to the intercept (zero) of 1:1 line explaining initiation of dry matter production simulations from the origin.

Table 6.5. Comparison of *TDM* model with experimental data for glasshouse (TCRU) and field experiments in Botswana and Swaziland for landraces S19-3, Uniswa Red, DipC and OM1.

Landrace	Number of observations	N-S	MAE	Slope	Intercept
Uniswa Red	57	0.662	100.106	0.816 ± 0.083	0.26 ± 0.11
S19-3	30	0.590	91.590	0.876 ± 0.141	0.22 ± 0.11
DipC	20	0.791	48.816	0.715 ± 0.039	-0.02 ± 0.05
OM1	19	0.731	49.076	0.712 ± 0.072	-0.08 ± 0.17

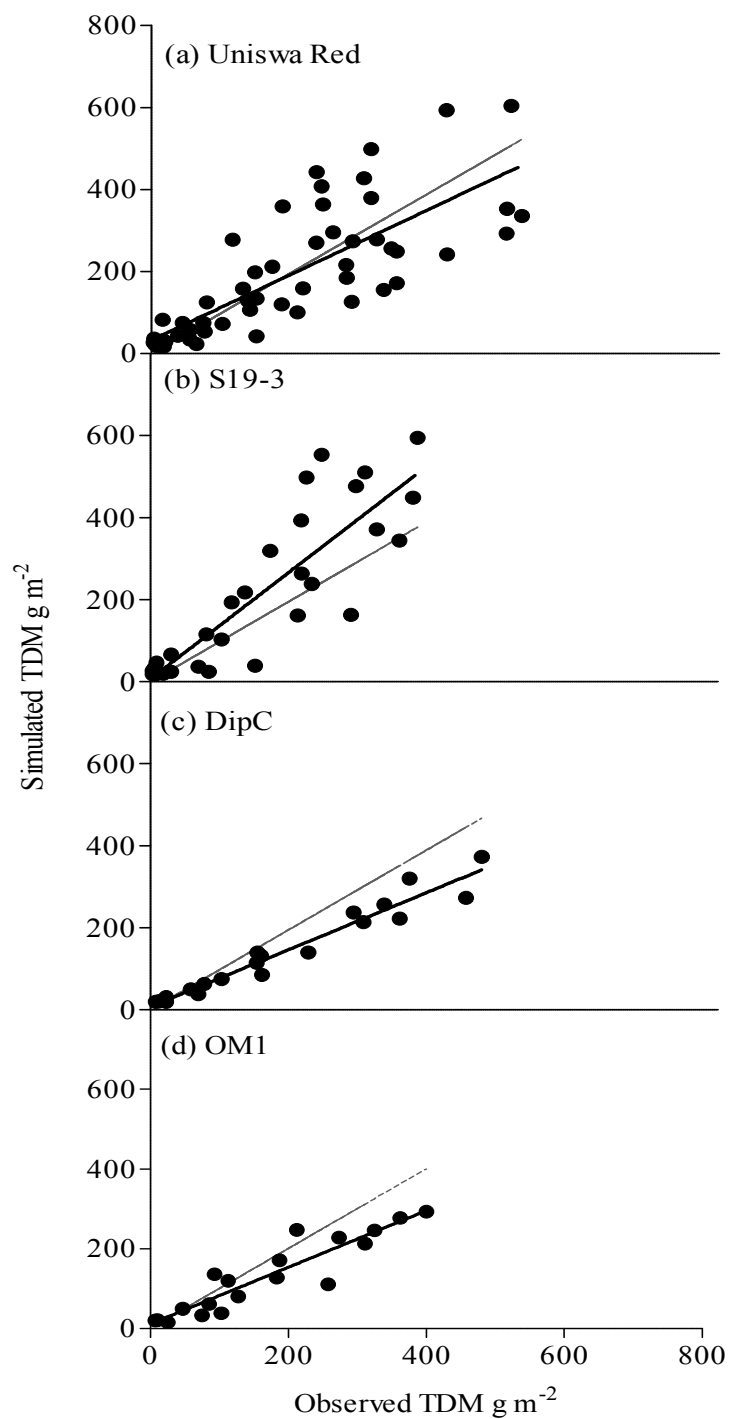


Figure 6.9. Comparison between measured and *TDM* for tested four landraces in glasshouse experiments, Nottingham, UK and field sites in Botswana (a) Uniswa Red (b) S19-3 (c) DipC (d) OM1 1:1 line (---) and regression line (—).

6.2.6 Yield Formation

The reported pod yield varied with temperature, soil moisture, photoperiod and landrace. The glasshouse experiments, showed that pod yield in Uniswa Red reduced at HT, exhibiting heat stress on pod formation. However, the Namibian landrace, S19-3, did not show the significant effect of temperature on pod yield. Drought reduced the yield in both landraces. BAMGRO was successful in simulating the pod yield under two temperatures; LT and HT and field conditions (TCRU: Figure 6.10; Botswana: Figure 6.11; Swaziland: Figure 6.12). The simulation results were statistically analysed to test the efficiency of model and the results are shown in Table 6.6.

Simulated pod yield correlated better with glasshouse measurements for S19-3 than Uniswa Red (Figure 6.10) with higher correlation (N-S varies from 0.88 to 0.98) and MAE less than 25 g m^{-2} (± 16 to 21 g m^{-2}). Similar comparison of pod yield simulations was observed in Uniswa Red (N-S varies from 0.72 to 0.80) but HT in the 2008 season reported an overestimation especially towards the end of the season so that the N-S was poorly explained in this case.

Pod yield varied with sowing dates and the model simulates the effect of variable climatic conditions in Botswana on yield formation (Figure 6.11). However, BAMGRO simulations for Botswana field grown landraces are not in good agreement with measured values with scattered data points.

As for *TDM* and *LAI*, BAMGRO was finally tested for two field trials in Swaziland (Malkerns and Luvu). Yield showed a strong variation with soil moisture which the model simulates successfully (Figure 6.12). The yield simulation for the drought affected Uniswa Red in Luvu experiment was well correlated with measured values having N-S, 0.91 and lower MAE $\pm 9.4 \text{ g m}^{-2}$. However it was underestimated at Malkerns where the crop experienced non limiting moisture environment. Similarly, DipC reported a poor correlation with

measured values. The observed yield of OM1 in Malkerns was well explained by the BAMGRO with N-S, 0.96.

Table 6.6. Comparison of *yield* model with experimental data for glasshouse (TCRU) and field experiments in Botswana and Swaziland.

Location/Experiment Treatment	Period	Number of observations	N-S	MAE
TCRU-glasshouse				
Uniswa Red: 23 ± 5 °C	2007	08	0.72	26.21
Uniswa Red: 33 ± 5 °C	2007	08	0.74	10.02
S91-3 : 23 ± 5 °C	2007	08	0.89	15.23
S91-3 : 33 ± 5 °C	2007	08	0.90	21.14
TCRU-glasshouse				
Uniswa Red : 23 ± 5 °C	2008	09	0.80	21.16
Uniswa Red : 33 ± 5 °C	2008	09	-0.42	11.99
S91-3 : 23 ± 5 °C	2008	09	0.88	15.66
S91-3 : 33 ± 5 °C	2008	09	0.98	15.79
Botswana				
Uniswa Red : Jan 18	2007	06	0.58	9.50
Uniswa Red : Feb1	2007	06	-67.524	17.628
DipC : Jan 18	2007	06	0.74	8.63
DipC : Feb 1	2007	06	0.057	3.486
OM1 : Jan 18	2007	06	-0.49	9.89
OM1 : Feb 1	2007	06	-6.462	6.530
Swaziland				
Uniswa Red:Malkerns	2002/03	13	-0.212	22.772
Uniswa Red: Luve	2002/03	12	0.913	9.430
DipC	2002/03	13	0.264	35.33
OM1 : Malkerns	2002/03	13	0.965	26.14

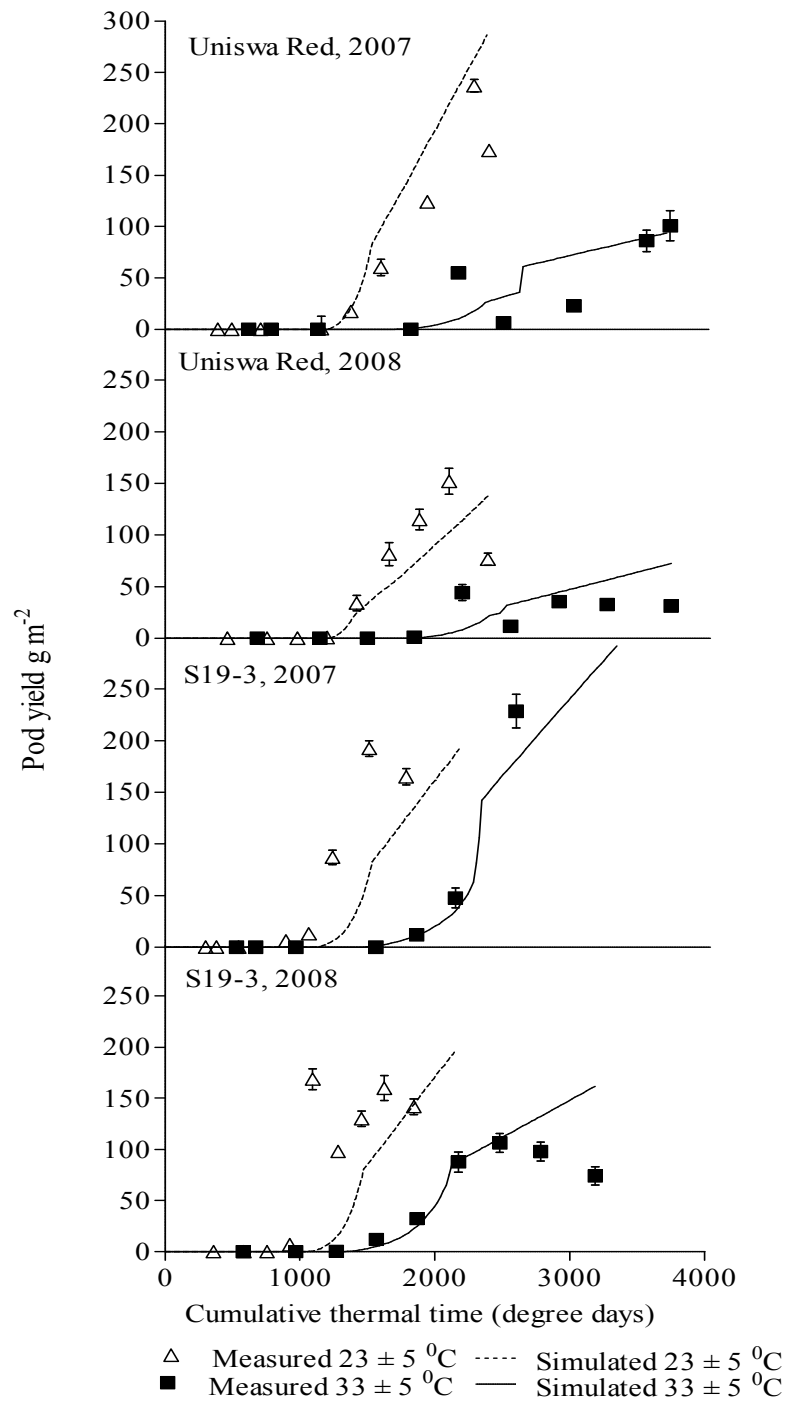


Figure 6. 10. Validation of yield(g m⁻²) with cumulative thermal time grown under glasshouse conditions for two bambara groundnut landraces Uniswa Red (a₁, a₂), S19-3 (b₁, b₂) with drought at 77 DAS (TCRU 2007) and 33 (TCRU-2008) respectively. Measured data are the average of twenty (23 ± 5 °C) and thirty (33 ± 5 °C) plants per landrace. Vertical bars are standard error (± SE).

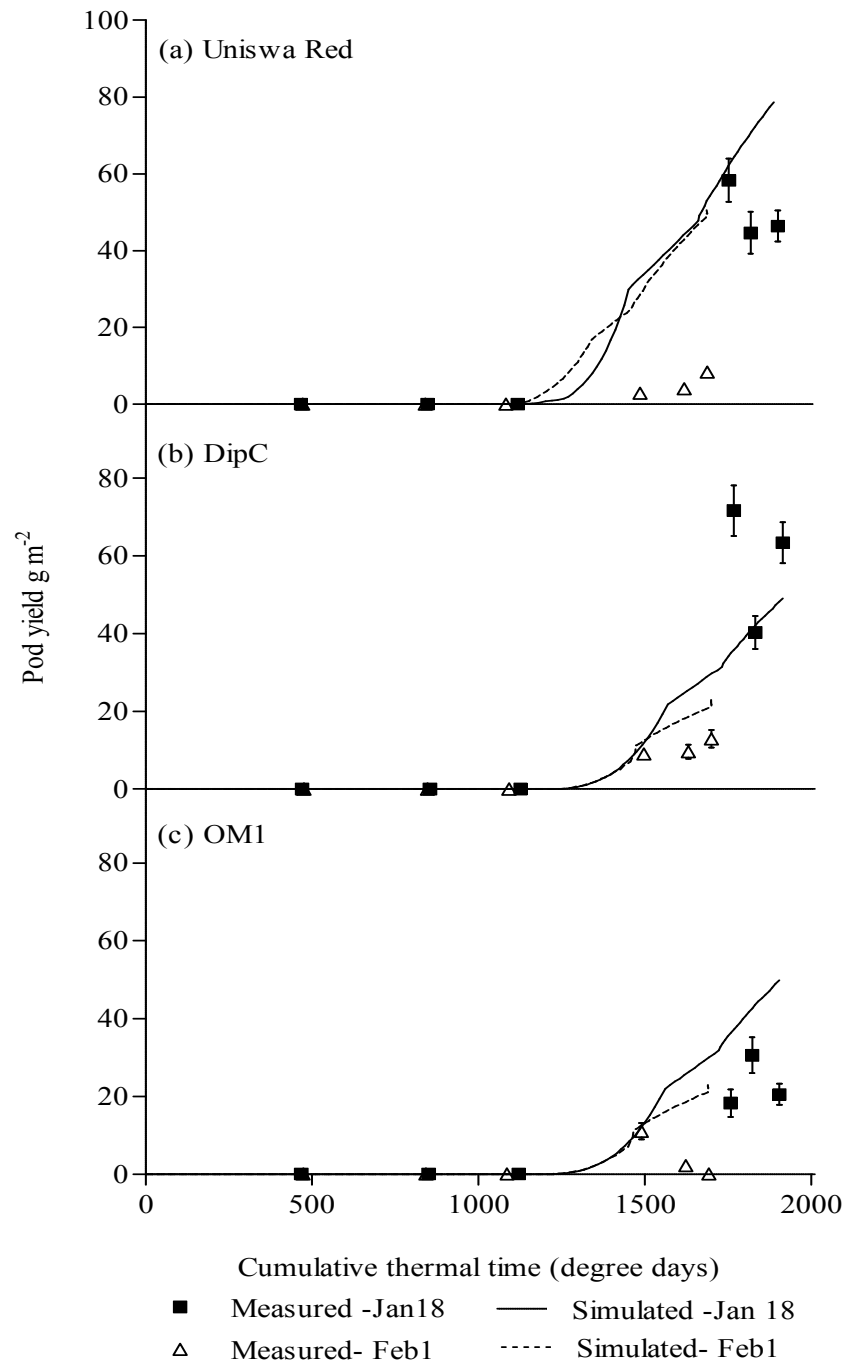


Figure 6. 11. Validation of yield (g m^{-2}) measured at field sites in Botswana for two sowing dates: January 18 and February 1 in growing season 2006/2007 for three bambara groundnut landraces (a) Uniswa Red (b) DipC (c) OM1. Measured data are the average of six plants per landrace. Vertical bars are standard error (\pm SE).

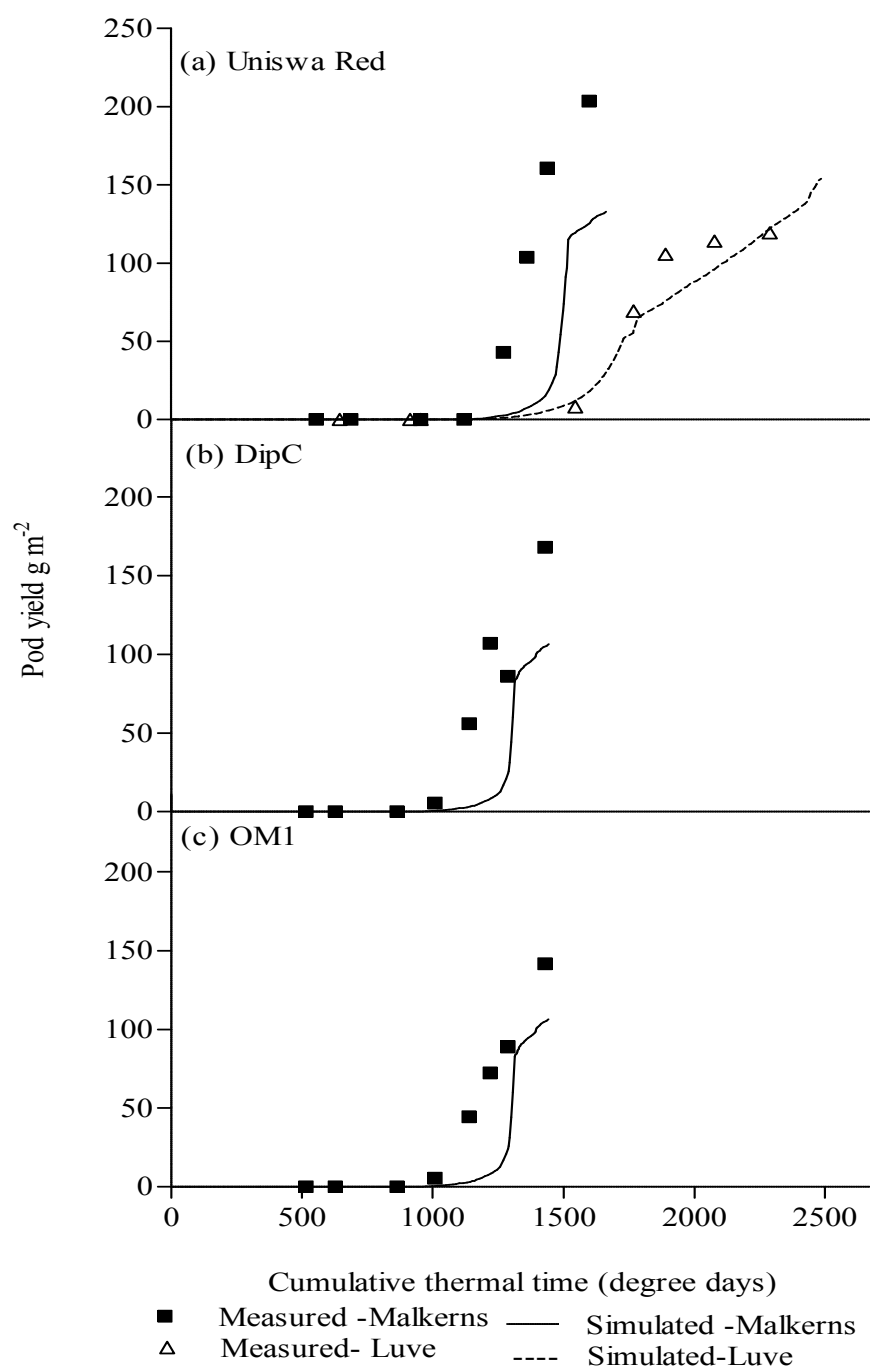


Figure 6.12. Validation of yield (g m^{-2}) measured at field sites in Swaziland Malkerns and Luve for three landraces for growing season 2002/2003 (a) Uniswa Red (b) DipC (c) OM1. Measured data are the average of ten plants per landrace. Measured data are average of ten plants per landrace.

The model comparison for pooled data on pod weight over the season for each landrace correlated well with measured values (Figure 6.13). The statistical comparison of the model for the four tested landraces (Uniswa Red, S19-3, DipC and OM1) is summarized in Table 6.7. Simulation of yield is well correlated with the line of identity (1:1 line) indicating acceptable correlation coefficient (N-S) for Uniswa Red (0.73) and S19-3 (0.87) (Table 6.7). The slope of the regression line in Uniswa Red (0.979 ± 0.066) and S19-3 (1.012 ± 0.061) are not significantly different from slope of one in 1:1 line. However, DipC (0.46) and OM1(0.50) reported poor correlation with 1:1 line and also significantly lower slope in the regression line when compared with the slope of 1 in 1:1 line. All four tested landraces the intercept of the regression line was not significantly different ($p > 0.001$) to the intercept (zero) of 1:1 line thus indicating the initiation of yield simulations through the origin.

Table 6.7. Comparison of *yield* model with experimental data for glasshouse (TCRU) and field experiments in Botswana and Swaziland for landraces S19-3, Uniswa Red, DipC and OM1.

Landrace	Number of observations	N-S	MAE	Slope	Intercept
Uniswa Red	57	0.73	16.32	0.97 ± 0.06	0.26 ± 0.11
S19-3	35	0.87	16.99	1.01 ± 0.06	0.22 ± 0.11
DipC	20	0.46	17.77	0.44 ± 0.07	-0.023 ± 0.05
OM1	19	0.50	15.62	0.49 ± 0.11	-0.08 ± 0.17

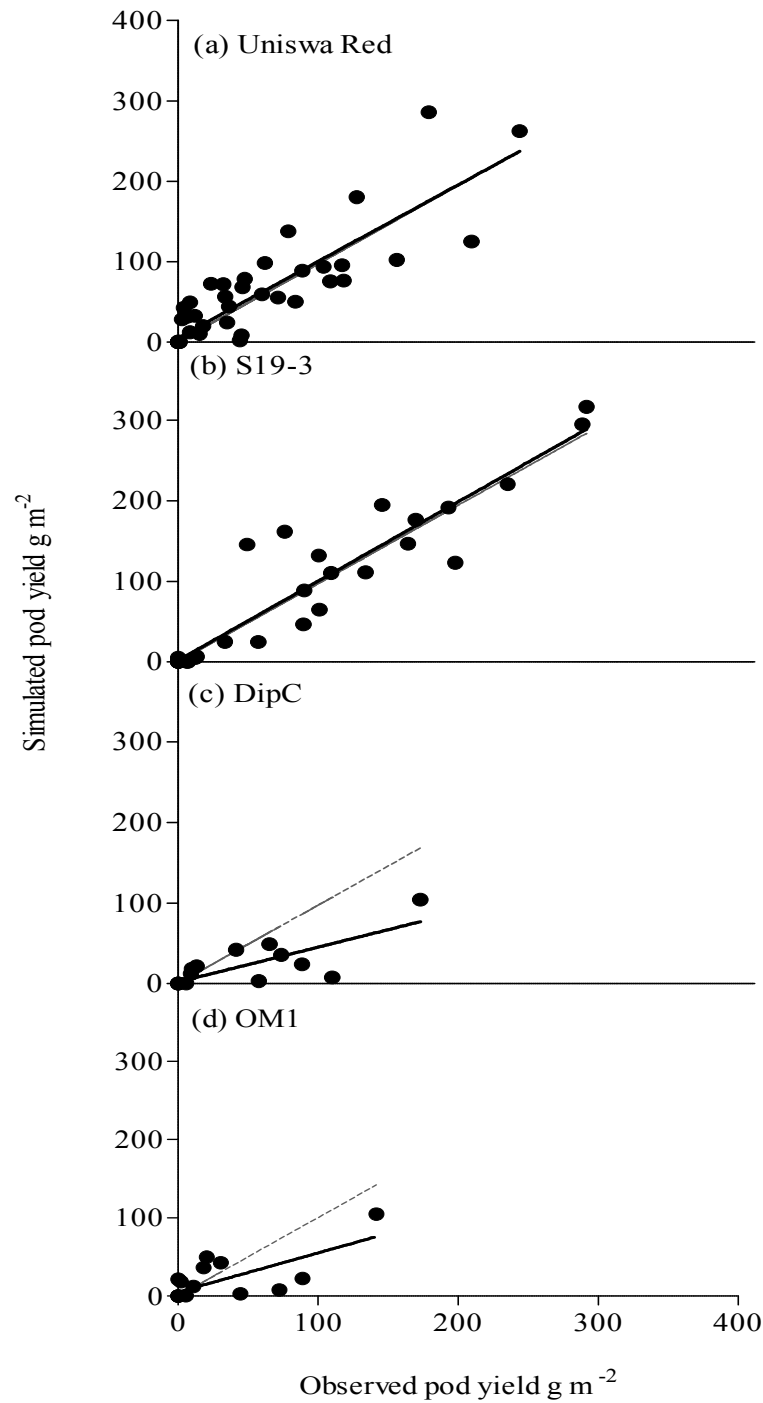


Figure 6.13. Comparison between measured and simulated *Yield* for tested four landraces in glasshouse experiments, Nottingham, UK and field sites in Botswana and Swaziland (a) Uniswa Red (b) S19-3 (c) DipC (d) OM1 1:1 line (---) and regression line (—).

6.4 CHAPTER SUMMARY

- A model for simulating biomass, dry matter partitioning and yield formation was developed in this study as a modified approach of previous bambara groundnut models and other classical crop simulation models. Summary of model Eqs. are 6.2, 6.3, 6.13, 6.14, 6.15, 6.16, 6.19, 6.20 and 6.21.
- The functions and relationships were derived from the glasshouse experiments at TCRU, University of Nottingham, UK and the model performance was validated with the experimental observations from glasshouse experiments and field trials in Botswana, and Swaziland.
- *TDM* simulations are well correlated with glasshouse data and Swaziland Malkerns (no water limitation). The model indicates general trend of *TDM* for two sowing dates in Botswana and Luvuvu site in Swaziland but the measured data shows a noticeable deviation.
- BAMGRO simulates pod yield for glasshouse data with higher correlation for Uniswa Red and S19-3. Swaziland field grown Uniswa Red and OM1 was well predicted by the model especially under drought. However, all three landraces reported poor correlation with measured values in Botswana.

CHAPTER 7

7.0 MODELLING THE ROOT GROWTH AND WATER UPTAKE OF BAMBARA GROUNDNUT FOR ABIOTIC STRESS

7.1 INTRODUCTION

The undoubted importance of water conditions for crop growth and development has been identified on many occasions (e.g. Roose, 2004). The rate of water uptake by the root system and the factors affecting the process of root growth are of fundamental interest in determining economic yield of a crop.

The unpredictable variability of climate especially with erratic distribution of annual rainfall in sub-Saharan Africa routinely causes severe yield losses. Therefore interest is growing in enhancement of the productivity of bambara groundnut landraces under marginal soil conditions where low-input agriculture is normally practiced. The drought tolerance capabilities of bambara groundnut have been characterised in many instances with commonly used growth indices such as, Leaf Area Index (*LAI*), Total Dry Matter (*TDM*) and yield (Collinson et al., 1996, 1997; Mwale et al., 2007a). Since monitoring root growth and distribution is both labour-intensive and expensive, attempts have made to develop models to simulate the root system (King et al. 2003; Manschadi et al. 1998).

The first dynamic crop model of bambara groundnut, BAMnut (Bannayan, 2001) followed the approaches of the CERES, family of models in which soil profile is divided into 3 layers and the root system restricted to the top and second layer. BAMFOOD project model (Cornelissen, 2005) used the water routine of the PALM model (Matthews, 2005) since no data were available on soil water content in the experiments used. It calculates the ratio between water supply and potential transpiration. The water supply component is influenced by the actual water content of the soil layers and the depth and distribution of the root system. However, Cornelissen

(2005) reported that the weakness in the soil water relations of the model created discrepancies with observed values of biomass and yield.

The present model, BAMGRO uses a simple approach to simulate the root growth, root distribution and soil water uptake of the crop under variable climatic conditions using the starting framework of wheat root model described by King et al., (2003). The model was primarily calibrated with glasshouse experiment (TCRU-2003), Nottingham and validated for glasshouse experiments (TCRU-2007, 2008) and field experiment in Notwane, Botswana (2007-2008 season) as per details explained in Chapter 3.

Therefore the objectives of the present study were to simulate (1) root growth and root distribution, (2) the water uptake by the root system and (3) the soil water balance of the profile under variable climates in controlled environments and in the field.

The model development is explained in section 7.2 together with suitable root data and parameterisation results. This is followed by model validation results (Section 7.3) and Chapter summary (section 7.4).

7.2 MODEL DEVELOPMENT AND PARAMETERISATION

The BAMGRO-soil water module uses daily time-steps to simulate root growth, root distribution, root water uptake and soil water balance from sowing until maturity for different bambara groundnut landraces. The parameters and relationships needed to build the functions in the model were derived from the glasshouse experiment-summer 2003 (Mwale, 2005), Nottingham, UK and published information (King et al, 2003).

The soil is represented as a one dimensional profile; it is homogeneous horizontally and consists of a number of soil layers. The total soil depth is assumed to be 1.5 m, divided into 15 soil layers each of 10 cm depth. This model

computes the daily changes to root length and balance of soil moisture content for each soil layer due to rainfall and irrigation, vertical drainage, soil surface evaporation and root water uptake processes.

7.2.1 Root Growth and Distribution

The present model is based on the following concepts: (1) The model captures the prevailing environmental conditions and resources from seed sowing to maturity, such that crop growth is restricted by water supply. (2) Root mass is initially predicted from the seed relocation of dry matter up to emergence, subsequently a fraction of dry matter is partitioned throughout the crop's life and this partitioning is set by a response to the environment. (3) The efficiency of water capture per unit root density remains constant during crop cycle (4) Complex physical processes in each soil layer are not considered in the BAMGRO-soil water module and soil bulk density (*BD*) is simply considered to determine Saturation Capacity (*SAT*), Field Capacity (*FC*) and Permanent Wilting Point (*PWP*). (5) Rooting depth is not restricted by the physical properties of the soil.

The root distribution is simulated according to Gale and Grigal (1987) as in Eq.7.1

$$Y = 1 - \beta^d \quad 7.1$$

Where,

Y = fraction of root system accumulated from soil surface to depth d

β = parameter to describe root distribution with depth

As β approaches 1, a higher proportion of roots are accumulated towards deeper layers. The cereal root model explains the stability of β during the main growth phase (mean \pm SE.; 0.953 ± 0.003) suggesting that root extension is maintained at a similar rate up to anthesis (King et al., 2003).

The BAMGRO-soil water module modifies the above approach assuming that the first day after sowing the value of β is zero and increases towards one at harvesting with an accumulation of thermal units, thus describing changes in root distribution through the profile. Glasshouse experiment-2003 (Mwale, 2005) provided root distribution data for 3 landraces; Uniswa Red (Swaziland), S19-3 (Namibia) and DipC (Botswana) at early growth (42 DAS), mid stage (84 DAS) and harvesting (142 DAS) (Figure.7.1). These data provided information to calibrate the model for those three landraces (Table 7.1). The parameters used to derive β are β_1 and β_2 according to Eq.7.2.

$$\beta = \beta_1 \times TT^{\beta_2} \quad 7.2$$

Where

β_1 and β_2 are landrace specific parameters (Table 7.1).

Table 7.1. The values for specific root weight and parameters to calculate β in three landraces.

Landrace	σ	β_1	β_2
Uniswa Red	1.648 ± 0.638	0.857	0.016
S19-3	1.732 ± 0.231	0.807	0.026
DipC	1.449 ± 0.378	0.741	0.038

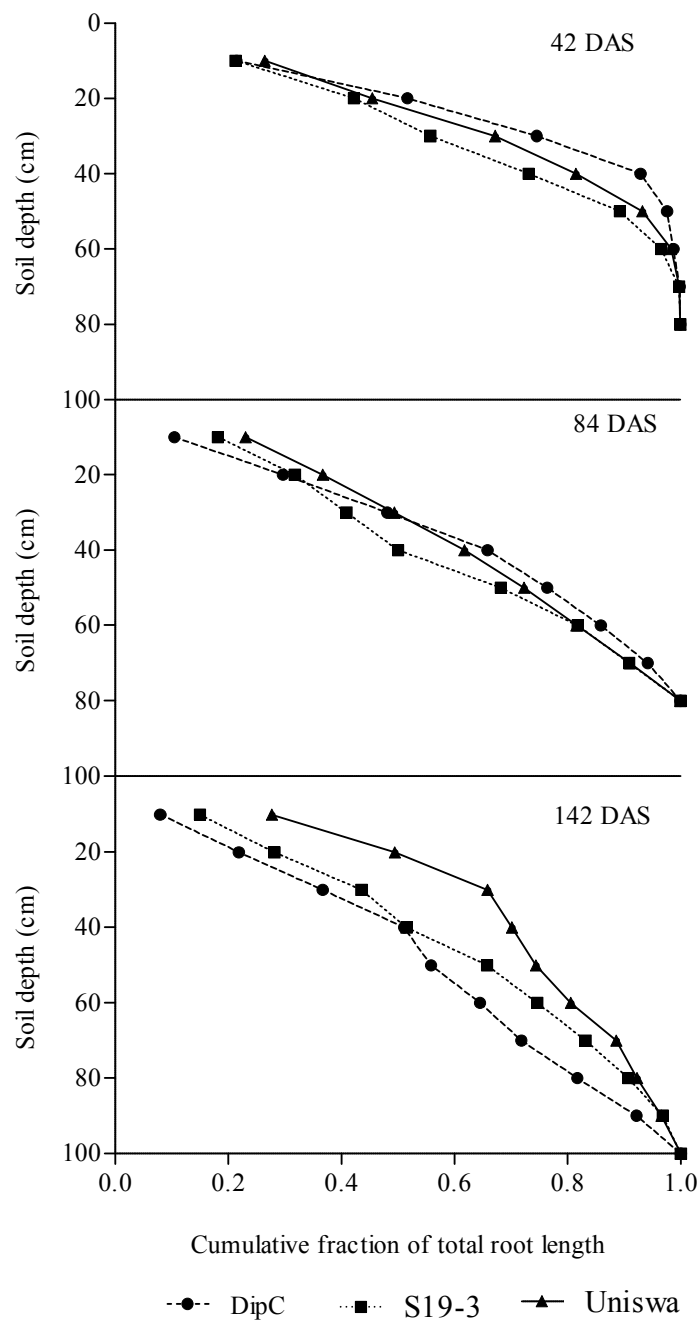


Figure. 7.1. Cumulative root length distribution at early growth (42 DAS), mid growth (84 DAS) and harvesting (142 DAS) in Uniswa Red, S19-3 and DipC.

The BAMGRO follows the cereal root model (King et al., 2003) to calculate root length density (L_v ; cm cm^{-3}). The value of β , σ (Table 7.2), RW (Chapter 6; Eq. 6.16) and Y (Eq. 7.1) are used to estimate the root length density of each 10 cm layer of the soil profile at each stage of crop growth according to Eq. 7.3. King et al., (2003) reported that total root length (L m) is related to root dry weight (RW g m^{-2}) by the specific root weight (σ g km^{-1}). According to experimental evidence the value of σ significantly varies among landraces (Table 7.1) (Mwale, 2005).

$$L_v = (Y_d - Y_{d-10}) \times \frac{RW}{\sigma} \quad 7.3$$

Where,

L_v	= root length density at 10 cm of soil layer at depth d (cm cm^{-3})
Y_d	= cumulative fraction of roots at depth d
Y_{d-10}	= cumulative root fraction at depth ($d-10$)
RW	= root weight ($\text{g m}^{-2} \text{d}^{-1}$)
σ	= specific root weight (g km^{-1})

7.2.2 Water Uptake

Potential water extraction from the soil by roots equals potential transpiration. Its magnitude depends on the depth and density of the root system, and on the available soil water. This maximum uptake rate can be realized in a soil that is at FC and fully exploited by roots. When either soil moisture or root density is below optimum the actual water uptake is reduced relative to potential. Following (King et al., 2003), a generic function (Eq.7.4) is used to predict water uptake as a fraction of total available water which is potentially available to uptake over the day. Thereby the potential water uptake for each 10 cm soil layer is estimated by Eq. 7.4 based on the maximum available water in each layer on a daily basis.

$$U_{pot(t)} = \theta \times (1 - \text{Exp}(-k_w \times L_v)) \times E \quad 7.4$$

Where,

- k_w = 'root water capture coefficient' (cm^2)
- L_v = root length density of the soil layer (cm cm^{-3})
- E = water capture parameter
- θ = fraction of available water in soil layer
- $U_{pot(t)}$ = change in potential water uptake in layer i (cm d^{-1})

The root water capture coefficient (k_w) is related to the resource uptake physiology especially molecular mechanism of water and nutrient transport across membranes and soil water transport mechanisms (King et al., 2003). Due to the lack of available data BAMGRO uses the value of two for k_w , similar to the value used for dry land barley (Gregory and Brown, 1989) and wheat (King et al., 2003). However, BAMGRO reduces k_w when the crop is exposed to temperatures below optimum ($T_{mean} < T_{opt}$).

The potential uptake by the whole root system is the accumulated capture by roots in each layer (1 to 15), assuming maximum possible rooting depth (1.5 m).

$$U_{pot(soil)} = \sum_{15}^1 \frac{dU_{pot(i)}}{dt} \quad 7.5$$

Then actual water uptake is calculated using the potential values as given by Eq. 7.8 considering Water Limited Growth (*WLG*) as in Eq. 7.6 and Light Limited Growth (*LLG*) as per details in Chapter 6 (Eq. 6.2). The actual water uptake from individual layer is calculated as a proportion of $U_{pot(soil)}$ and U_{actual} (Eq. 7.8).

$$WLG = \frac{(U_{pot(soil)} \times TE)}{SD} \quad 7.6$$

$$U_{actual} = \left(\min \left(\frac{LLG}{WLG}, 1 \right) \right) \times U_{pot(soil)} \quad 7.7$$

$$U_i = \left(\frac{U_{actual}}{U_{pot(soil)}} \right) \times U_{pot(i)} \quad 7.8$$

Where,

- U_{actual} = actual rate of water uptake by roots in profile (mm d⁻¹)
 $U_{pot(soil)}$ = potential rate of water uptake by roots in profile (mm d⁻¹)
 U_i = actual rate of water uptake by roots in layer i (mm d⁻¹)
 TE = transpiration efficiency (g mm⁻¹)

7.2.3 Soil water balance

As mentioned earlier, the model assumes 15 soil layers of 10 cm. Soil moisture is calculated separately for each of these (Figure 7.2). Layer 1 is the topmost layer dealing with calculation of potential evaporation from soil, addition from rainfall and irrigation, water extraction from crop component and vertical drainage. The subsequent layers deal with water extraction from roots and vertical drainage.

Layer 1

The soil water module requires calculation of potential evaporation from the soil surface. This is done according to the CERES family of models. The calculations of the evapotranspiration are taken primarily from the work of (Ritchie, 1972) but daily rate of potential evapotranspiration ($EVAP O_{pot}$) is calculated using an equilibrium evaporation concept as modified by Priestley and Taylor (1972) that represents a theoretical limit for the crop considered, expressed as a function of the environment. The amount of evaporation depends on soil properties and environmental conditions. To avoid the complexities of data input to the Penman type equations, Class A Pan evaporation has been used for BAMGRO-soil water module as a modified version of the Jones and Kiniry approach (1986), which

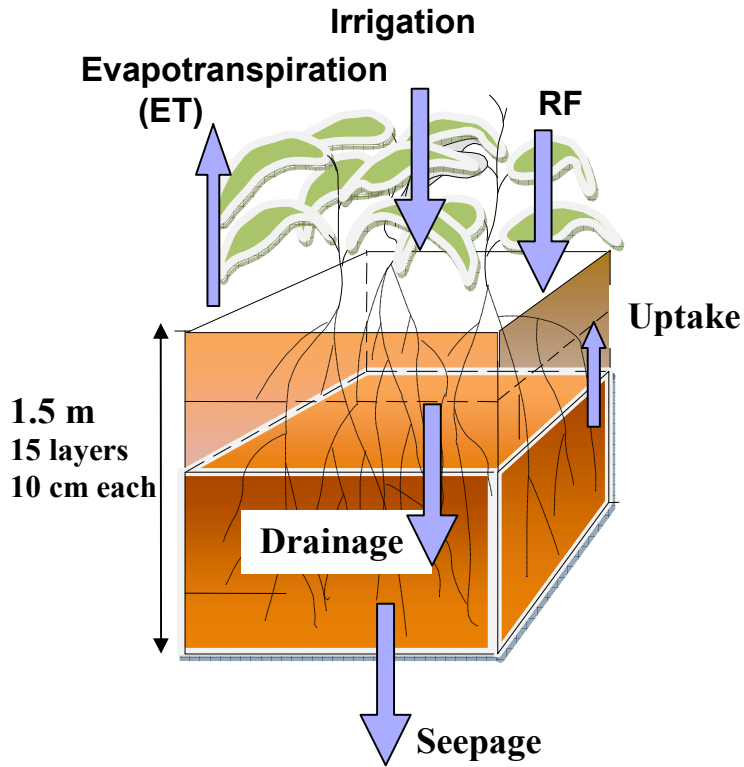


Figure 7.2. Inward and outward water flows for the different layers considered in the soil water balance.

utilizes the fractional interception (f ; Eq. 6.4). Therefore rate of change in potential evaporation ($EVAPO_{pot}$) and actual evaporation ($EVAPO$) from the soil surface is given by Eq. 7.9 and 7.10 respectively.

$$EVAPO_{pot} = PanE \times (1 - f) \quad 7.9$$

$$EVAPO = (EVAPO_{pot}) \times \frac{(WATER_1)}{(FC_{layer})} \quad 7.10$$

Where,

$EVAP_{pot}$	= potential evaporation (mm d ⁻¹)
$EVAP$	= the actual evaporation (mm d ⁻¹)
$WATER_l$	= amount of soil moisture in layer 1 (mm)
FC_{layer}	= the soil moisture at field capacity in layer 1(mm)
$PanE$	= pan evaporation (mm d ⁻¹)

To estimate infiltration the model takes the simplified approach in which the top layer takes up water until it is at field capacity. Subsequent water is added directly to the second layer (Eq. 7.12). The drainage component and FC_{layer} are estimated according to Eq. 7.12.

$$\frac{dWATER_l}{dt} = IRRI + RAIN - DR_l - EVAP - UP_l \quad 7.11$$

$$DR_l = \max((WATER_l - FC_l), 0) \quad 7.12$$

$$FC_l = FC_{soil} \times d_l \quad 7.13$$

Where,

$WATER_l$	= soil moisture in layer 1(mm)
$IRRI$	= irrigation (mm d ⁻¹)
$RAIN$	= precipitation (mm d ⁻¹)
UP_l	= actual water uptake by roots in layer 1(mm d ⁻¹)
DR_l	= drainage in layer 1(mm d ⁻¹)
d_l	= depth of layer soil layer (cm)
FC_l	= field capacity in layer 1 (cm)

Layers 2 to 15

If the soil moisture in the adjacent upper layer exceeds its *FC* the excess water flows to the subsequent layer of the soil profile. The major component in soil water balance in layers 2 to 15 is due to the uptake of water by the crop (Figure 7.2). In addition, excess water is directed to the next lower layer as the drainage fraction as explained in layer 1 (Eq. 7.12). The soil water balance in layer 2 to 15 is given by Eq. (7.14).

$$\frac{dWATER_i}{dt} = DR_i - DR_{i+1} - UP_i \quad 7.14$$

Where,

$WATER_i$ = soil moisture in layer i (mm)

UP_i = actual water uptake by roots in layer i (mm d⁻¹)

DR_i = drainage in layer i (mm d⁻¹)

7.3 MODEL VALIDATION

The model was validated only for soil moisture due to the unavailability of root growth data. Mainly the model was compared with experimental soil moisture data sets from glasshouse experiments in 2007 and 2008 and the Botswana 2007/2008 season. The available soil moisture is assumed to be the net remaining after water uptake, vertical drainage and evapotranspiration. Therefore the simulation results of root growth and distribution though the profile are shown as they are connected to soil water uptake component (Figure 7.3 and 7.4).

7.3.1 Root Growth and Distribution

The fraction of the root system accumulated at each depth is shown in Figure 7.3 for Uniswa Red (as an illustration) grown under 23 ± 5 °C and 33 ± 5 °C at glasshouse condition (TCRU) in 2007. According to Figure 7.3, high temperature simulates a higher root growth rate compared to low temperature in 2007. A similar pattern is simulated for Namibian landrace, S19-3 (simulation results not shown).

A similar relationship is found for root length density (L_v). Plants grown under high temperature achieve maximum L_v at earlier stages of growth whereas low temperature indicates further increase in L_v with accumulation of thermal units (Figure 7.4). Although the present study is not validating the simulation against the root data due to unavailability of root data, it could be done if the necessary data becomes available.

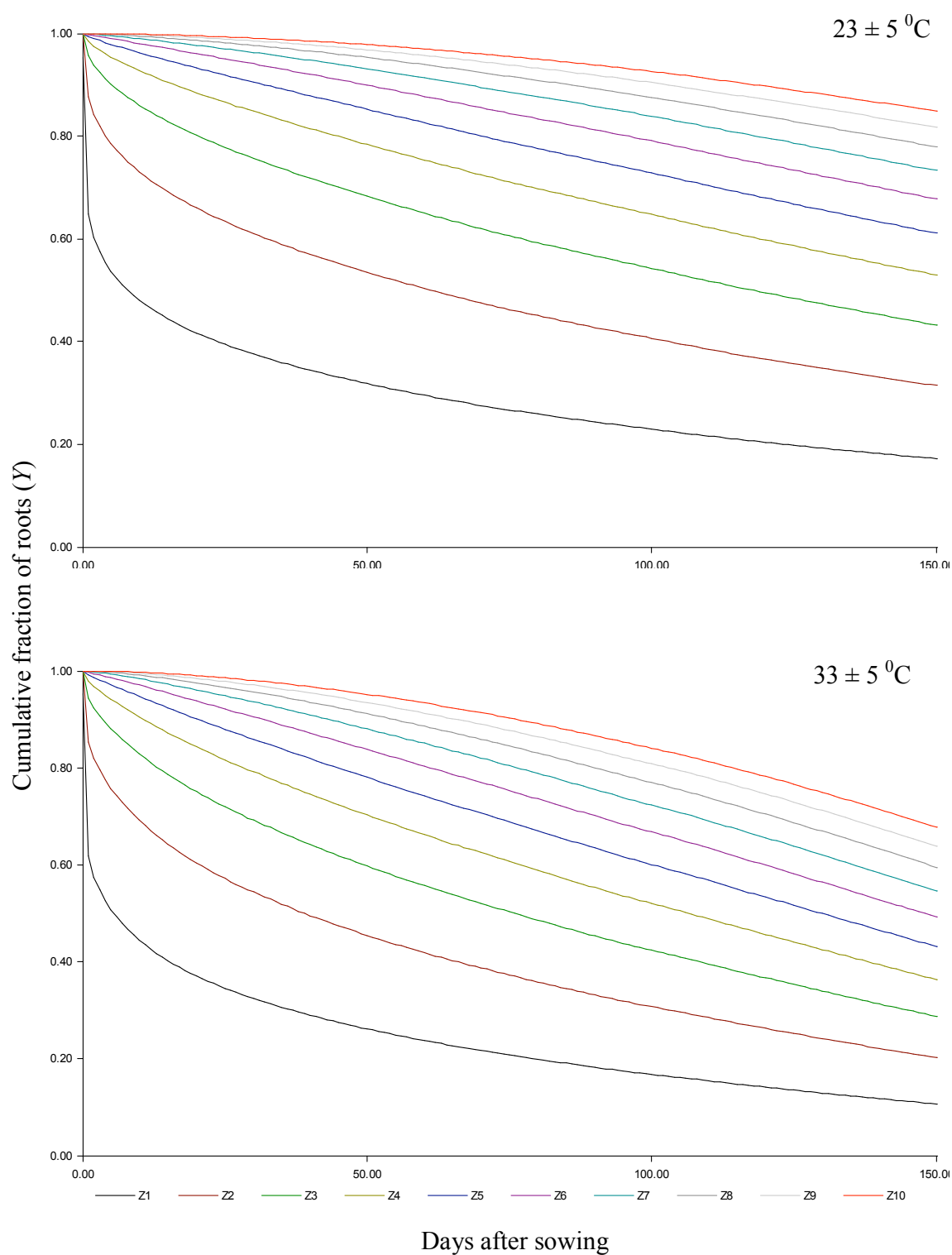


Figure 7.3. Simulation results for fraction of root distribution (Y) of Uniswa Red grown under $23 \pm 5^\circ\text{C}$ (a) and $33 \pm 5^\circ\text{C}$ (b) in Glasshouse experiments during 2007.

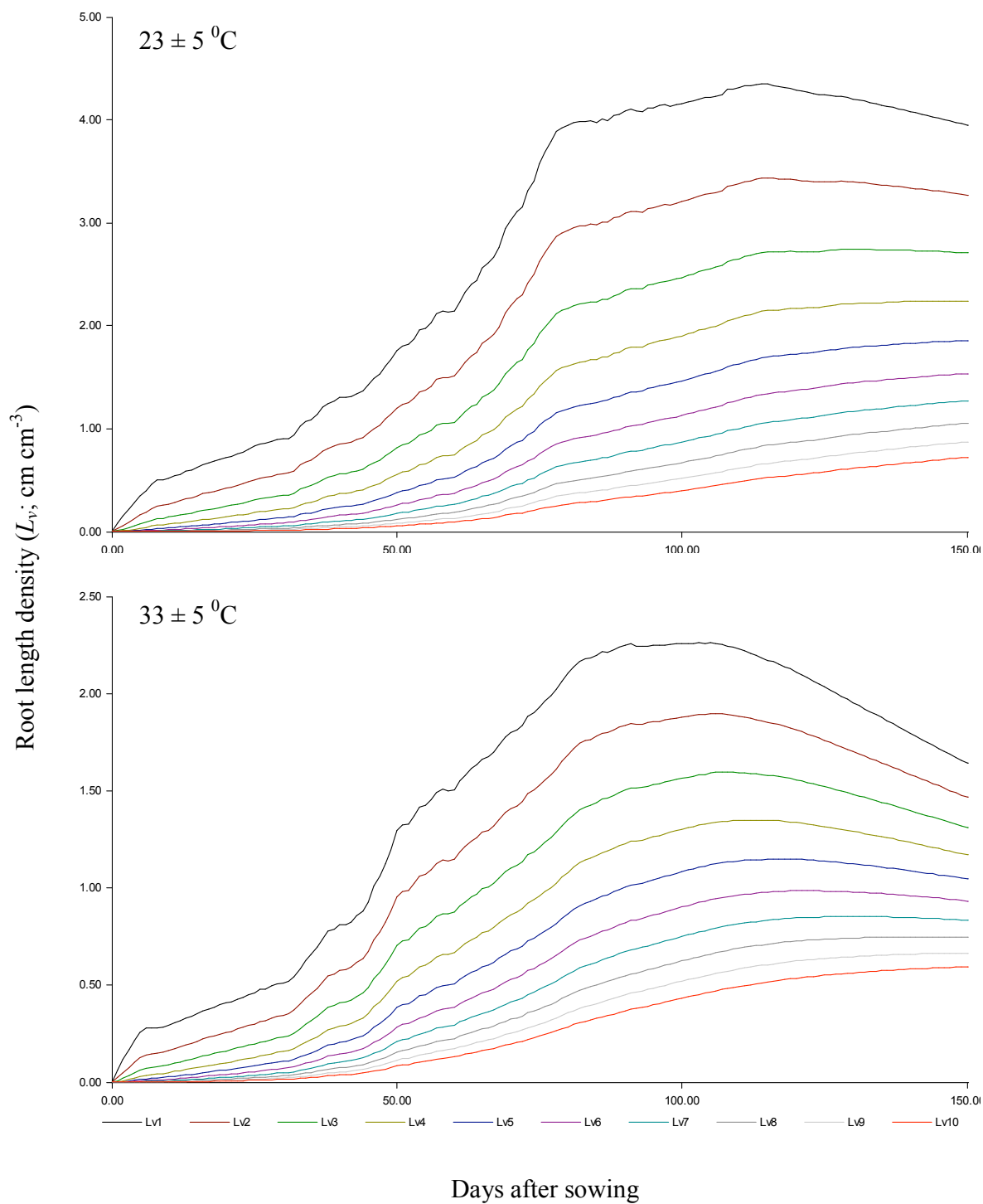


Figure 7.4. Simulation results for root length density (L_v) of Uniswa Red grown under $23 \pm 5 ^\circ\text{C}$ (a) and $33 \pm 5 ^\circ\text{C}$ (b) in Glasshouse experiments during 2007.

7.3.2 Soil Water Balance

Comparison between simulated and observed soil moisture content (mm) for four soil layers (layer 1, 10 cm; layer 2, 20 cm; layer 3, 30 cm; layer 10, 100 cm) in glasshouse experiments during summer months of 2007 and 2008 are shown in Figure 7.5, 7.6, 7.7 and 7.8 respectively for two tested landraces: Uniswa Red and S19-3.

The model was able to simulate the reduction in soil moisture content (mm) correctly due to the drought (2007, 77 DAS; 2008, 33 DAS). However the predicted soil moisture content (mm) in deeper layers was heavily under estimated, particularly under high temperature (33 ± 5 °C) thus indicating over estimation of losses of the water from the layer 10 (100 cm) (Eq. 7.11 and 7.14).

A similar trend was observed for the variation of soil moisture content (mm) for S19-3 (Figure 7.7 and Figure 7.8). However the model generally over estimated the soil moisture content in the 2008 glasshouse experiment in which the drought was imposed at 33 DAS.

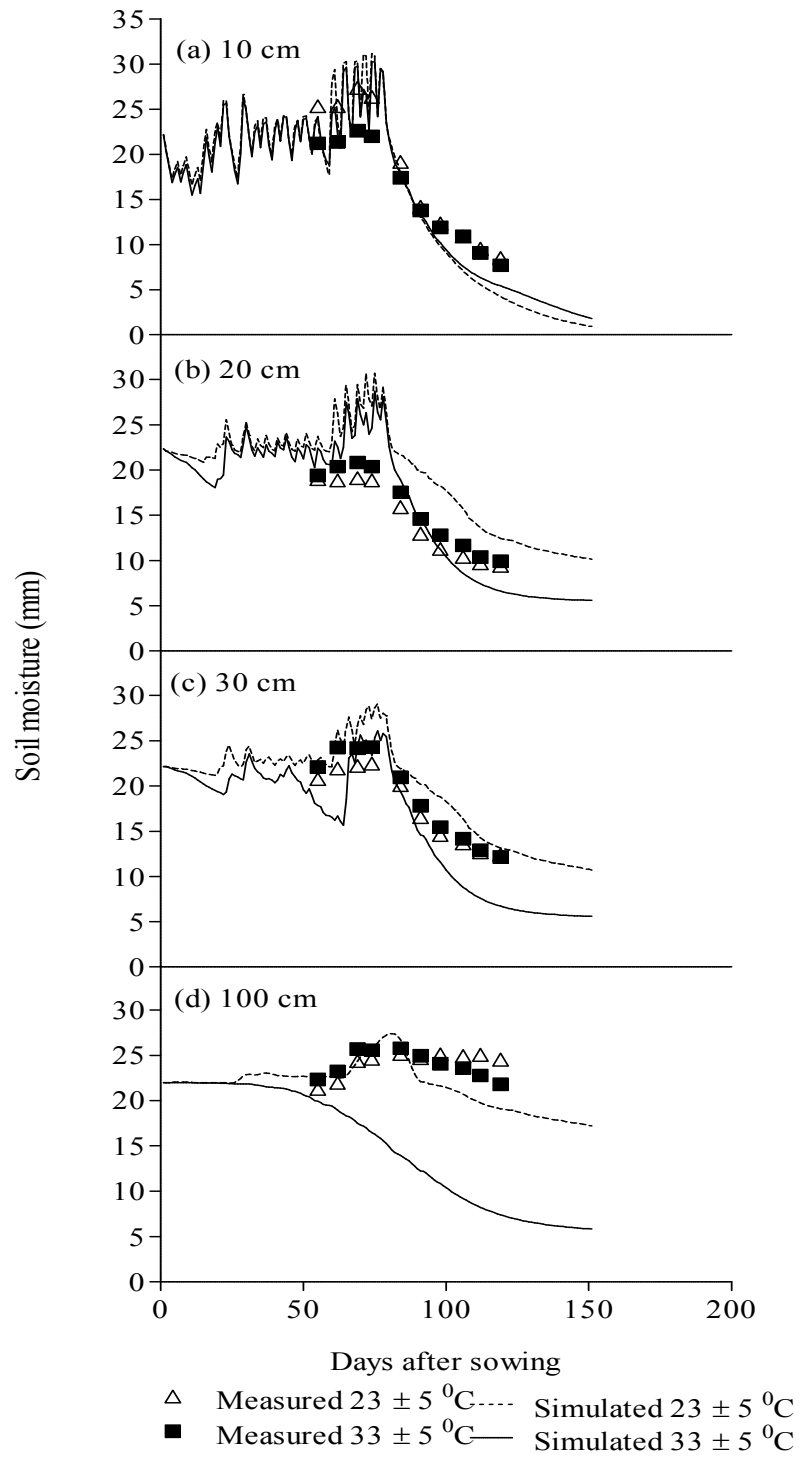


Figure. 7.5. Soil moisture variation with days after sowing at top 10 cm (a), 20 cm (b), 30cm (c) and 100 cm (d) layers for Uniswa Red grown under $23 \pm 5^{\circ}\text{C}$ and $33 \pm 5^{\circ}\text{C}$ in Glasshouse experiments during 2007.

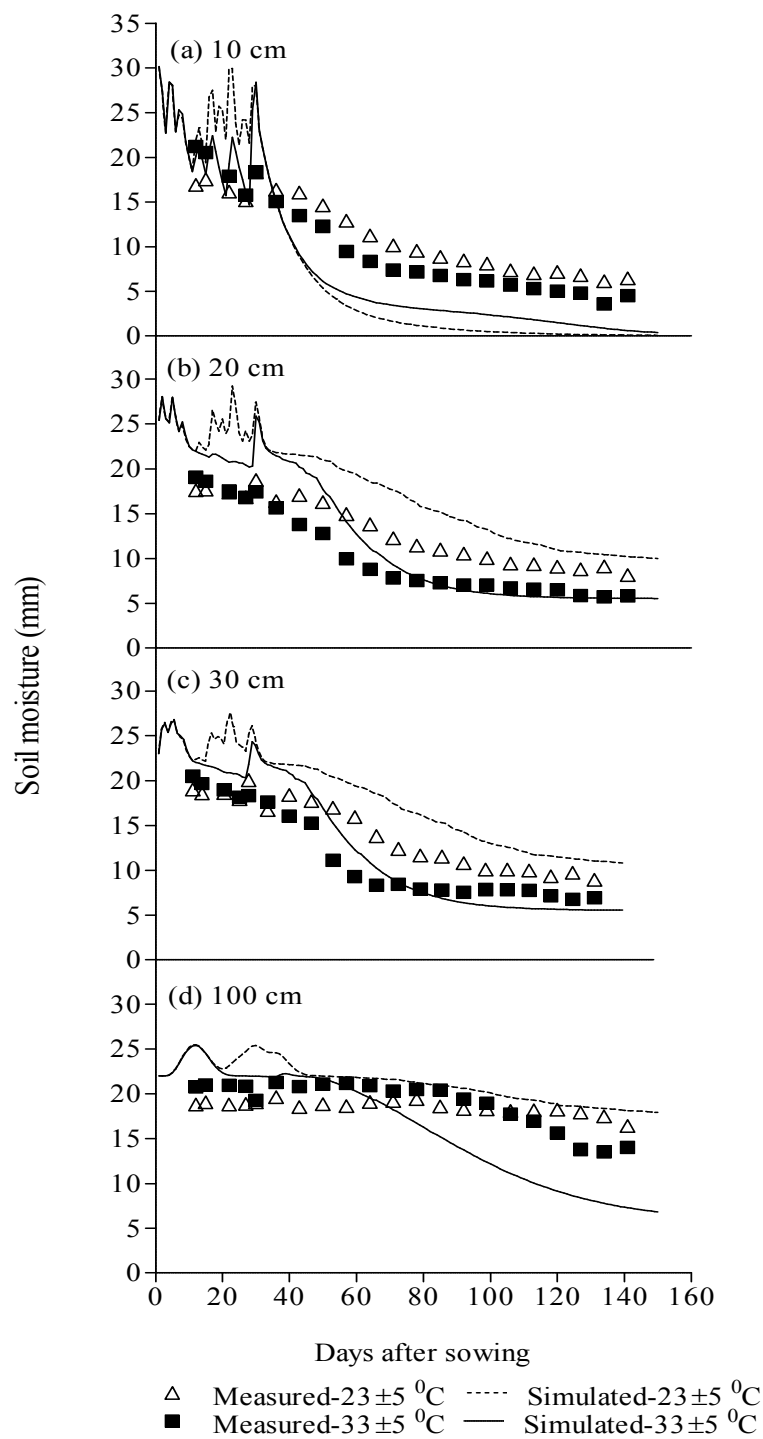


Figure. 7.6 Soil moisture variation with days after sowing at top 10 cm (a), 20 cm (b), 30cm (c) and 100 cm (d) layers for Uniswa Red grown under $23 \pm 5^{\circ}\text{C}$ and $33 \pm 5^{\circ}\text{C}$ in Glasshouse experiments during 2008.

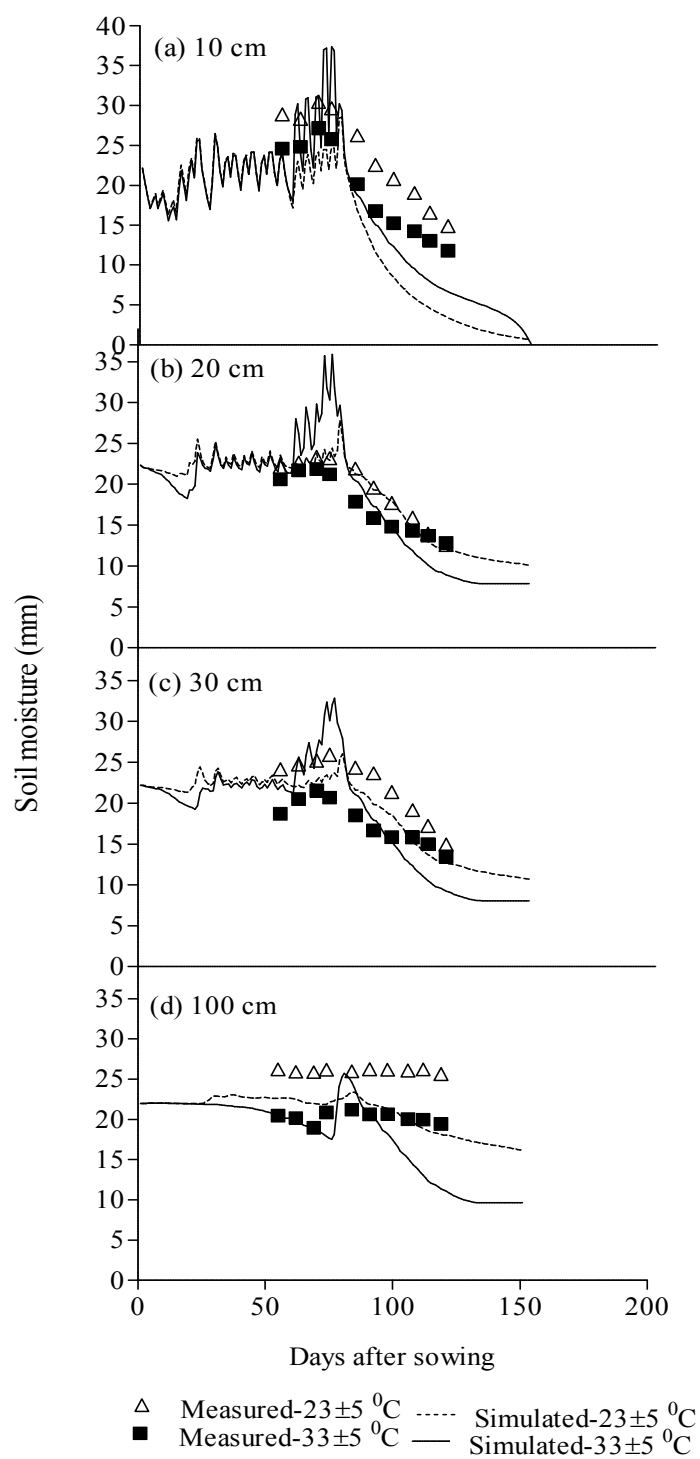


Figure. 7.7. Soil moisture variation with days after sowing at top 10 cm (a), 20 cm (b), 30cm (c) and 100 cm (d) layers for S19-3 grown under $23 \pm 5^\circ\text{C}$ and $33 \pm 5^\circ\text{C}$ in Glasshouse experiments during 2007.

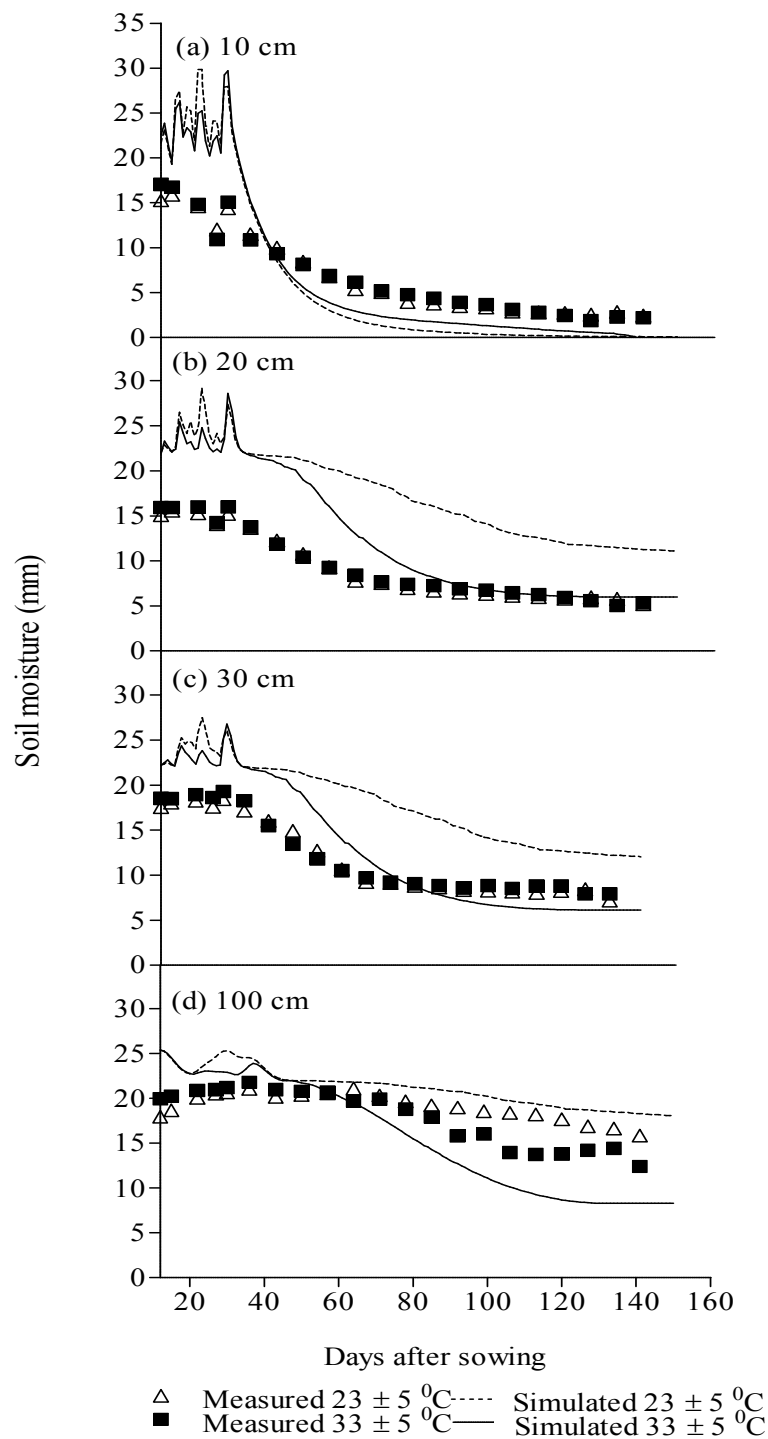


Figure. 7.8. Soil moisture variation with days after sowing at top 10 cm (a), 20 cm (b), 30cm (c) and 100 cm (d) layers for S19-3 grown under $23 \pm 5^\circ\text{C}$ and $33 \pm 5^\circ\text{C}$ in Glasshouse experiments during 2008.

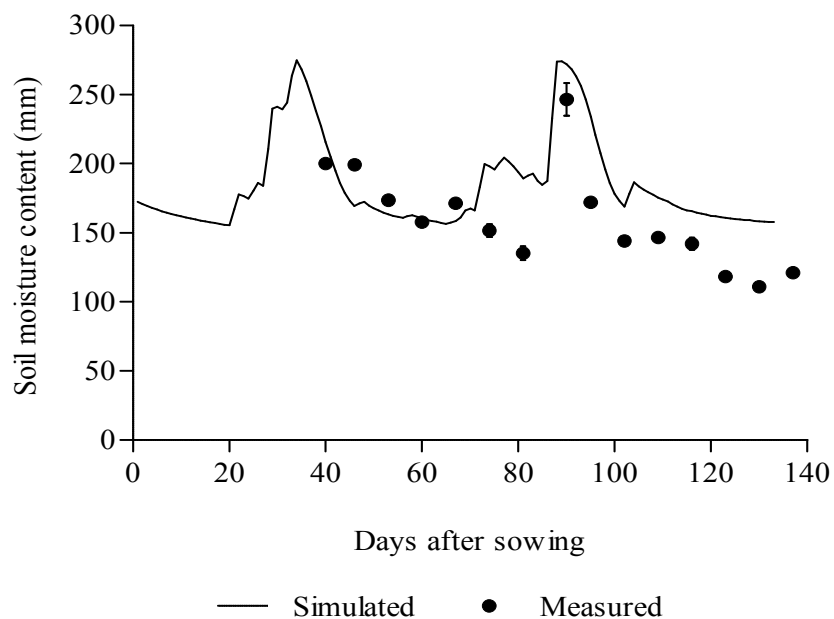


Figure. 7.9. Soil moisture variation of Uniswa Red with days after sowing through the soil profile in Botswana field site during the growing season 2007-2008. The soil moisture was measured using neutron probe.

BAMGRO-soil water module simulates the soil moisture variation the soil profile of field sites in Notwane, Botswana with less deviation from measured values (MAE is ± 22.8 mm) (Figure 7.9). However, there is an over estimation especially towards the end of the growing season.

7.4 CHAPTER SUMMARY

- A model for simulation of root growth, distribution and plant water uptake developed by this study is a modified approach of a simple wheat model. The summarised model Eqs. are 7.1, 7.3, 7.5, 7.6, 7.9, 7.11 and 7.14.
- The functions and relationships were derived from the glasshouse experiments at TCRU, University of Nottingham, UK.
- The testing the model performance was primarily done with the experimental observations from glasshouse experiments and field trials in Botswana.
- BAMGRO-soil water model predicts the soil water content for two bambara groundnut landraces (Uniswa Red, S19-3) realistically but need further improvement in calibration of k_w , β and ϵ_s .

CHAPTER 8

8. DISCUSSION

This thesis describes model results for canopy development (leaf number and *LAI*; Chapter 5), dry matter production (*TDM*; Chapter 6), yield (pod weight; Chapter 6) and soil moisture (Chapter 7) for two contrasting landraces (Uniswa Red, S19-3) for glasshouse studies and three landraces (Uniswa Red, DipC and OM1) for field sites in Botswana and Swaziland. The model validation results demonstrate deviations of model predictions for two different growth conditions (glasshouse and field) under drought, heat and cold stress. The possible reasons for these discrepancies by means of crop physiology, landrace variability, agro-ecological adaptations and modelling approaches are explained below (section 8.1, section 8.3, section 8.4, section 8.5). This is followed by the potential uses of present study (section 8.6), pathways for future development of BAMGRO (section 8.7) and major conclusions (section 8.8).

8.1 ENVIRONMENTAL CONDITIONS OF MODEL DATA SETS

BAMGRO was mainly calibrated by glasshouse data, Nottingham, UK which made it possible to conduct most of the physiological measurements in a country whose climatic conditions would not be suitable to grow bambara groundnut in the field. In addition, the use of controlled environment glasshouses made it possible to evaluate the response to one or two abiotic stress factors at a time, while keeping others constant. Although air temperature, saturation deficit and soil moisture are controlled within the TCRU glasshouses, the experiments were conducted under natural light during UK summer. The intensity of solar radiation during the summer months in Nottingham is spread over 16 h of day length providing approximately 50% less intensity compared to the original environment of the two landraces (Uniswa Red and S19-3) in sub-Saharan Africa. Therefore, the growth and yield performances of tested landraces may have not reached their

potential in the glasshouse environments in Nottingham resulting in inadequately estimated parameters. The parameterisation of BAMGRO with glasshouse data has probably contributed to the deviation of simulation results for Africa field sites.

8.2 AGRO-ECOLOGICAL ADAPTATIONS AND LANDRACE VARIABILITY

The present study uses four landraces originated in three zones in semi-arid Africa (Uniswa Red-Swaziland, S19-3-Namibia, DipC and OM1-Botswana). According to the experimental evidence from the present study (TCRU-2006, 2007, 2008) and previous studies (Mwale, 2007a and 2007b) the Namibian landrace, S19-3 showed a faster rate of development, which led to earlier maturity and also reported relatively better economy of water use compared to other landraces. In contrast, Uniswa Red was slow growing and lagged behind S19-3 and DipC (Mwale, 2005) in most of the physiological traits. In addition, the glasshouse experimental results from the present study showed significant reduction of pod formation in Uniswa Red when grown under high temperature ($33 \pm 5^{\circ}\text{C}$) compared to S19-3 (Plate 8.1). According to the detailed evaluation of responses of Uniswa Red, S19-3 and DipC for drought, Mwale (2007a and 2007b) reported that, S19-3 short phenology and fast development may reflect its adaptation to low rainfall (365 mm mean annual rainfall) and warm conditions with short growing period. Whereas Uniswa Red showed its agro-ecological adaptation to relatively cooler, high rainfall (1390 mm mean annual rainfall) conditions having longer growing period. The Botswanian climate is similar to Namibia but with a slightly longer growing period (527 mm mean annual rainfall).

The rainfall amounts, the daily mean temperatures and lengths of growing seasons in these countries appears to be closely related to the growth and developmental performances of the landraces used in the present study and shows their agro-ecological adaptation. Based on the climates of Namibia, Swaziland and Botswana, it is obvious that bambara groundnut has a wider climatic adaptation.

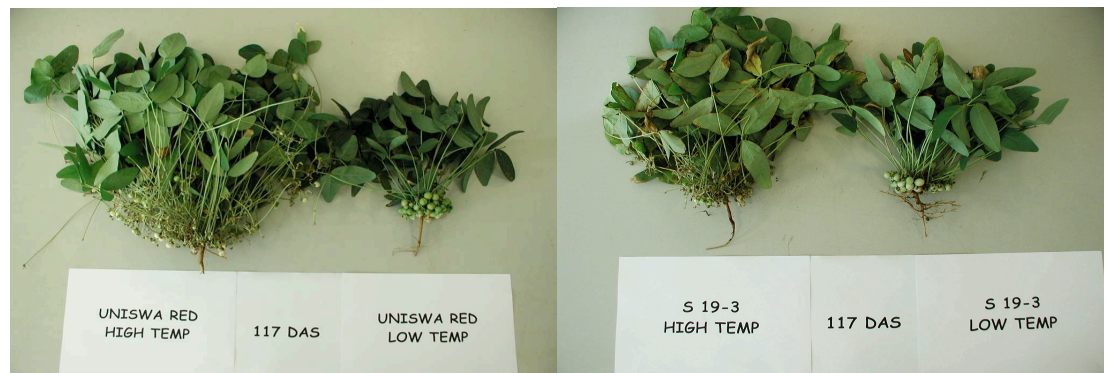


Plate 8.1. The pod formation of Uniswa Red and S19-3 in response to temperature. The results from glasshouse experiment, Nottingham, UK in 2006.

The deviation of model predictions from measured values can be further explained by the landrace variability (BAMLINK-on going work, Sean Mayes personal communication). Bambara groundnut landraces are expected to exist as a series of inbred lines, with the variability between lines dependent upon the genetic width of the parent materials. For most of the landraces, adaptive traits (number of days to flowering, number of days to maturity) are likely to be reasonably constant; due to the adaptation of the landrace to their original environment in which it is regularly grown and selected by farmers. However, there is a possibility that genes for agronomic traits may be highly variable between different inbred lines of a landrace. Having an estimate of ‘genetic width’ of a landrace the intra-landrace variability has to be considered within the selected landraces for the present study. Initial analysis of five individual plants from two landraces (Uniswa Red and S19-3) with fourteen microsatellites identified three microsatellites which showed allelic variation in Uniswa Red (ten alleles) and none in S19-3, suggesting that ‘genetic width’ of S19-3 is narrower than Uniswa Red. Also larger scale investigations are underway, with the long term aim to develop a multiplexed SSR-based estimate of genetic diversity within a landrace (Personal communications Sean Mayes).

8.3 CANOPY DEVELOPMENT

The modified model of canopy development accounting for abiotic stress described in Chapter 5 presents a more mechanistic platform than previous models (BAMFOOD project-Cornelissen, 2005; BamNut-Banyan, 2001) in which to incorporate temperature, soil moisture and photoperiod responses into a comprehensive canopy development. Bambara groundnut is a photoperiod sensitive crop therefore canopy development is modelled in response to the combined effect of temperature and photoperiod.

Canopy development of bambara groundnut varied primarily due to differences in air temperature, soil moisture and photoperiod. This large variation in canopy development through appearance, expansion and senescence of leaves was accurately reproduced in simulations. Cold and drought stress are simulated as a reduced rate of leaf production while heat stress and increase in photoperiod simulated higher rate of leaf production resulted in improved correlation with measurements for different genotypes in glasshouse, UK, Botswana (Notwane) and Swaziland (Malkern and Luve).

Model simulations indicate significantly higher rate of daily leaf production (Figure 5.5) and *LAI* (Figure 5.7) for HT (33 ± 5 °C) compared to LT (23 ± 5 °C) under glasshouse conditions in Nottingham, UK for tested two landraces (Uniswa Red and S19-3). The function for the daily rate of leaf production (Eq. 5.3) that is calculated as the balance between daily rate of new leaf production (Eq. 5.4) and daily rate of senescence (Eq. 5.14) simulates wider gap between two temperatures (LT and HT) for Uniswa Red compared to S19-3 and is well correlated with measured values. The Gaussian function developed in BAMGRO for the rate of new leaf production (Eq. 5.4) successfully captures the major abiotic stress (heat, cold and drought) by means of stress index (K_{s_i}) (Eqs. 5.5, 5.6). However, the overestimation of leaf number for both Uniswa Red (HT) and S19-3 (LT) in 2007 season under glasshouse condition are difficult to explain as those two situations coincide with late drought (77 DAS) and heat and cold stress. Considering the

agro-ecological adaptations of the landrace, this over estimation may be due to the poor representation by the model of the interaction between extreme temperatures and late season drought. The incorporation of day length factor (DL_{fac}) within the rate of new leaf production function provides pathways to simulate increased rate of leaf production when the crop is grown in the day lengths above 12 h. Moreover, model for new leaf production accounts the differences in planting densities through density factor (Eq. 5.7). Since LAI (Eq. 5.16) is dependent on rate of leaf production, BAMGRO was capable of predicting the variation of LAI successfully over the growing season under heat, cold and drought stress for tested landraces: Uniswa Red (TCRU-2007, TCRU 2008, Swaziland-Malkerns); S19-3 (TCRU-2007, TCRU-2208); DipC (Swaziland-Malkerns); OM1 (Swaziland-Malkerns). However, there is a follow up effect of leaf number on LAI with over estimation especially for Uniswa Red (HT) in 2007. The simulation of canopy development in field sites under drought in Swaziland (Luve) and Botswana was generally poor for the three landraces (Uniswa Red, Dipc and OM1). The main reason for poor model simulations in the field sites in Botswana may be due to the fact that the differences in growing environment in glasshouse conditions, Nottingham, UK from which the parameters were derived. Environmental conditions in Swaziland (Malkerns) during the growing season (2002-2003) were mild and were closer to UK summer (2002, 2006) rather than Botswana. In addition the intra-landrace variability that is not considered in BAMGRO may have contributed to this discrepancy.

The previous modelling attempts on bambara groundnut (BAMFOOD project) were unable to simulate the canopy development accurately under water limited situation due to the lack of regulation of rate of leaf production under drought stress. Cornelissen (2005) clearly demonstrates the lack of a slowing effect of rate of leaf production under drought stress especially at the early stages of growth cycle. The model developed in the present study (BAMGRO) successfully addressed this issue especially during early growth.

There is limited published information on the role of temperature for the rate of leaf appearance (Massawe et al., 2003) and role of photoperiod on canopy development (Brink, 1997) of bambara groundnut landraces. The functions and relationships developed within the present study can be further improved more comprehensively with thorough understanding of physiological mechanisms of temperature and photoperiod by means of suitable experiments.

In classical crop simulation models, in the absence of photoperiodic effects the leaf production is successfully modelled by a thermal time approach (Wheeler et al., 1999). In most crop growth models, leaf area is derived from the relationship between temperature and rate of leaf appearance, leaf number and individual leaf area (Bonnett, 1998). For example, the plant leaf area of pigeonpea was analysed with functional relationship between thermal time and main stem node appearance, between main stem nodes and leaves per plant, the distribution of individual leaf area by node, and between leaf senescence and thermal time (Ranganathan et al., 2001). Most potato models estimate leaf area expansion rate as an exponential function of cumulative thermal time (Fleisher and Timlin, 2006). The CERES-Sorghum model estimates potential leaf area expansion as a function of leaf tip position on the main stem and genotypic specific maximum expansion rate using a Gompertz relationship (Thornley and Johnson, 1990).

8.4 DRY MATTER PRODUCTION AND YIELD

8.4.1 Dry Matter Production

BAMGRO uses a simple approach to simulate biomass production (Eq. 6.3) considering limitation of radiation (LLG) and soil water supply (WLG). LLG is mainly dependant on light extinction coefficient (k), conversion efficiency of intercepted radiation (ϵ_s) and canopy cover (LAI) where as WLG (Eq. 7.6) is determined by various soil and root growth characteristics of the crop (Chapter 7). Use of water productivity function to calculate the dry matter production based on the potential water uptake by the root system (Eq. 7.5) when the crop is exposed

to drought stress ($0 \leq \text{WSTRESS} \leq 1$) is an improvement from previous modelling (BAMnut and BAMFOOD project) on bambara groundnut. Therefore BAMGRO provides opportunities to account for the differences in potential water uptake by the root system that is primarily dependent upon root growth, distribution and k_w ('resource capture coefficient') of the considered landrace as per details explained in Chapter 7.

However, the model validation results from glasshouse experiments, Nottingham, UK reported an overall overestimation of dry matter under water limitation especially towards the end of the season for LT ($23 \pm 5^\circ\text{C}$) in both landraces. In contrast, field experiments in Malkerns, Swaziland (no water limitation) show a good correlation (r^2 varies 0.65 in Uniswa Red and 0.76 in OM1) between simulated and measured *TDM*. The biomass for the field in Swaziland is simulated using *LLG* function (Eq. 6.2) as there was no water limitation in Malkerns during the experimental period, and the model prediction is in good agreement. The crop sown in two sowing dates, January 18 and February 1 in Botswana showed a statistically acceptable model validation results in *TDM* for Uniswa Red (N-S, 0.86 to 0.88) and DipC (N-S, 0.72 to 0.81) under poor rainfall. Therefore the dry matter production functions under water limiting and non-limiting *LLG* produced a satisfactory simulations for field sites in Africa while glasshouse experiments in Nottingham, UK reported a significant over estimation under LT ($23 \pm 5^\circ\text{C}$) when associated with water limitation. The difficulty in gaining good agreement between simulated and measured total biomass (*TDM*) under drought condition associated with LT ($23 \pm 5^\circ\text{C}$) for S19-3 and Uniswa Red perhaps may be the impact of cold stress on root growth, root distribution and k_w ('resource capture coefficient') which is not thoroughly understood within BAMGRO.

However the effect of cold stress on dry matter production can be further explained by radiation use efficiency (ϵ_s). According to the results from glasshouse experiments in Nottingham, UK, ϵ_s varies with temperature in the two contrasting landraces (Uniswa Red and S19-3) used in the present study. Generally LT ($23 \pm 5^\circ\text{C}$) caused a reduction in ϵ_s in both landraces of approximately 32% and 55% in

Uniswa Red and S19-3 respectively. This experimental data explains a reduction of radiation use by the crop under LT (23 ± 5 °C) is severe in Namibian landrace, S19-3 indicating cold stress. The estimated ϵ_s of 1.5 g MJ^{-1} under high temperature condition is lower than that recorded in previous experiments in glasshouse experiments, Nottingham, UK. Mwale et al.(2007a) reported that ϵ_s varies from 1.19 to 1.66 g MJ^{-1} for different landraces under drought and irrigated treatments respectively for 2001 and 2002 seasons in Nottingham, UK. Previous TCRU experimental results (Chapter 3) for bambara groundnut reported that drought reduced ϵ_s from 1.51 g MJ^{-1} to 1.02 g MJ^{-1} across landraces. However observed values at HT (33 ± 5 °C) from the present study are in agreement with irrigated treatments in the literature, including Collinson et al.(1996) (ranges between 1.0 and 2.8 g MJ^{-1}), with significantly lower values under LT (23 ± 5 °C). It has been reported that ϵ_s is dependent on crop development stage and declines during the grain filling period because of the remobilization (Muchow and Sinclair 1994). In the absence of resource limitations and pest and diseases in chickpea ϵ_s is constant during whole crop cycle (Soltani et al., 2006). However ϵ_s is sensitive to ambient temperature and vapour pressure deficit (Kiniry et al., 1998).

A similar approach was used in calculating biomass production within the first dynamic model on bambara groundnut, BAMnut (Bannayan, 2001) considering *LLG* and *WLG*. However, the use of saturation deficit (*SD*) as a normalising factor for temperature, in calculating *WLG* (Eq. 7.8) adjusts the transpiration equivalent ($TE \text{ g kg}^{-1} \text{ kPa}^{-1}$) for variable temperatures within BAMGRO. In addition, biomass production in the present study is advancement from previous BAMFOOD project model (Cornelissen, 2005) that used a simple modifier to adjust the total dry matter production function under water limited condition and does not account the root and soil characteristics in detail.

Various crop models for major crops have used the similar approaches as in BAMGRO to simulate the actual daily biomass considering the minimum of two potential growth rates as *LLG* and *WLG*. Robertson et al. (2001) reported a crop

simulation model for pigeonpea (*Cajanus cajan* (L.) Millspaugh) and the transpiration demand are modelled as a function of current day's crop growth rate, divided by the transpiration use efficiency. Also pigeonpea model used transpiration use efficiency as 5 g kg kPa^{-1} which is common to most of the tropical legumes. A crop simulation model for common beans calculates the dry matter production under soil water limited condition by a water stress factor that was derived from the total water potential (combination of matric and osmotic potentials) (Adiku et al., 2001).

8.4.2 Yield Formation

BAMGRO uses a simple approach to simulate the rate of change of pod number (Eq. 6.19) as an inverse relationship with the rate of leaf production so that the cumulative effect of temperature, soil moisture and photoperiod is accounted successfully. When pod formation starts the dry matter partition is the leading process as explained by Marcelis (1993a) with potential demand with priority function. However the daily rate of pod filling is regulated by a maximum pod filling rate ($0.4\text{-}0.5 \text{ mg d}^{-1}$) assigned to the model. Overall simulation of pod weight over the growing season is well correlated with measured values under glasshouse conditions and in field condition in Swaziland in which the effect of abiotic stress factors is encountered. Significantly higher predicted pod weight compared to measured values in glasshouse experiment 2007 under LT ($23 \pm 5 \text{ }^{\circ}\text{C}$) for Uniswa Red is not possible to explain with the available information. Consistently poor simulation of pod weight for Botswana was found for all three landraces (Uniswa Red, DipC and OM1). Intra-landrace variability can be a possible reason for this deviation.

The earlier model developed in BAMFOOD project uses a landrace-specific linear relation to calculate the rate of increase in the weight of the pods ($\text{g phenochron}^{-1} \text{ plant}^{-1}$) with accumulation of phenochrons, when the podding stage is reached. Also it calculates a constant multiplier when the photoperiod is longer than 12 h to slow down the advancement of the pod filling stage, preventing the formation of

yield. However this model does not account for the landrace variability in photoperiod effect due to the lack of information on day length.

A pigeonpea model simulates the partitioning fractions towards pod wall, pods based on the order of priority between pods, pod wall and vegetative parts (Robertson et al., 2001). Also demand for assimilates in formation of pods is driven using cultivar-specific daily rate of harvest index (*HI*) increased towards a genotypic maximum.

8.5 SOIL WATER MODULE

The BAMGRO-soil water module provides a framework for predicting root growth, water uptake and soil water balance for bambara groundnut landraces grown under heat, cold and drought stress conditions. Due to limited data on root growth and distribution, model parameters are not very specific to bambara groundnut, especially the value for k_w (water capture coefficient) was taken from dry land barley (King et al. 2003). Generally the model overestimate the soil moisture content in upper soil layers and it is heavily under estimated at deeper layers. There are several possibilities for these discrepancies.

According to the model, the vertical distribution of roots (Y) as described by β , can influence the water uptake capacity of the crop. The general over estimation of the simulation results from the present study indicates that the values used for β are too high. As this was derived from the crop grown at optimum temperature condition (28 ± 5 °C), a general reduction of β can be hypothesised under heat and cold stress. However, this has not been considered within the model due to the lack of information on changes of β under different temperature stress conditions. In addition, the use of a single value of β from sowing to harvesting, does not consider the root distribution with age. The value used for (k_w) is also not very specific to bambara groundnut and this may contribute towards the poor correlation of model simulations with the measured data.

The model clearly indicates the relationship of root length density (L_v) and water uptake (Eq. 7.4). However the variation of L_v under drought, heat and cold stress for bambara groundnut is unknown. Husain et al. (1990) indicates that both L_v and rooting depth of faba bean (*Vicia faba* L.) grown under drought stress were significantly higher than regularly irrigated crops. A study focussed on investigation of L_v and water uptake revealed that some cereal species consistently had five to ten times the total root length of grain legumes and a higher correlation with maximum rooting depth than the root length density (Hamblin, 1987).

The use of generic parameter values of cereals within BAMGRO model leads to uncertain predictions in root growth distribution. In addition, several soil physical factors influence root growth and distribution that are not considered in BAMGRO (eg. hydraulic conductivity, soil porosity).

8.6 POTENTIAL APPLICATIONS OF RESULTS

1. BAMGRO provides facilities to match different landraces to most suitable agro-ecological regions in Africa. As the present study used two contrasting landraces (Uniswa Red-Swaziland, S19-3-Namibia) mainly to represent the extremes of climatic conditions prevailing in semi-arid Africa, the user can position the new landraces considering average rainfall and temperature records of that particular region relative to Swaziland and Namibia. The most effective way of positioning landraces is clustering them based on daily mean temperatures and mean annual rainfall of the original growing region and select one from each cluster to calibrate BAMGRO. This will provide the user to better understanding of growth and yield performance of that particular cluster for considered location.
2. BAMGRO can be successfully used in planning management practices considering the critical growth stages that are susceptible to abiotic stress. For instance, BAMGRO provides information on reduction of canopy cover, dry matter production thereby the yield under heat, cold and drought

stress. So that the user can adjust the planting dates to overcome this unfavourable weather during the growing period as much as possible. In addition, as the pod formation is retarded by the day length when exceeds the 12 h during the pod filling stage, the user can schedule the cropping calendar to overcome longer day lengths during the pod filling stage.

3. The results of BAMGRO model have already been incorporated within the interface of AquaCrop the UN-Food and Agriculture Organization (FAO crop-model) that is used to simulate yield response to water of several herbaceous crops. This is a companion tool for a wide range of users with minimum data sets and applications including yield prediction under climate change scenarios (<http://www.fao.org/nr/water/aquacrop.html>). Similarly, BAMGRO can be included to the established cropping system interface- Decision Support System for Agrotechnology Transfer (DSSAT) (Jones et al., 2003) as sub crop files in CROPGRO. DSSAT has already showed a success with SOYGRO and PNUTGRO making very straight forward procedures.
4. The current modelling aspects in bambara groundnut provided the scientific evidence for developing a mathematical framework to predict growth and yield so that this work can be used as a key model for other underutilised crops that have genetically variable landraces rather than genetically improved varieties or cultivars.

8.7 FUTURE DEVELOPMENT OF BAMGRO

The development of a crop simulation model for an underutilised crop, bambara groundnut, is very difficult due to the unavailability of consistent data sets from landraces and poor infrastructure in most of the field locations in Africa. Therefore, the present work could not address some of the issues due to the restricted time frame and limited funding. There are some issues that can be addressed for further extension of the current work as outlined below.

1. The effects of differences in the quality/quantity, of solar radiation in field sites in semi-arid Africa and glasshouse environments in Nottingham, UK are not well understood and no approach has been attempted to quantify this aspect. Therefore one practical approach to understand and overcome the effect of variability due to solar radiation is to conduct detailed field experiments in contrasting radiation environments to calibrate BAMGRO for Uniswa Red and S19-3. Meanwhile BAMGRO can proceed with two categories for field and glasshouse experiments in future validations.
2. In the previous model (BAMFOOD project) the photoperiodic effect on pod formation was modelled using a linear reduction in accumulation of phenochrons when day length exceeds 12 h. However, this was based on a hypothetical constant linear reduction. According to the experimental evidences in the present study the multiplier used to calculate phenochrons accumulation should be non-linear. The implementation of this non-linearity in the model gives rise to noticeable changes in the rate of phenochron accumulation as day length exceeds 12 h. This has not been extensively tested and should be a worthwhile area for future study.

3. Currently, there is no detailed information about the cardinal temperatures: base (T_{base}), optimum (T_{opt}) and ceiling (T_{high}) for Uniswa Red and S19-3. The previous model (BAMFOOD project) used 9.9 °C, 30 °C and 42 °C as base, optimum and ceiling temperatures across all the landraces. But careful analysis of results in Mwale (2005) PhD thesis and agro-ecological adaptations of Uniswa Red and S19-3 the cardinal temperatures were adjusted in the present study. Therefore it uses 8.5 °C, 28 °C and 38 °C for Uniswa Red and 12 °C, 30 °C and 45 °C for S19-3 as base, optimum and ceiling temperatures assuming Swaziland landrace (Uniswa Red) is more adjusted to lower temperatures compared to Namibian landrace (S19-3) (Figure 8.1). Therefore it is useful to do proper experiments to estimate cardinal temperatures for Uniswa Red and S19-3.

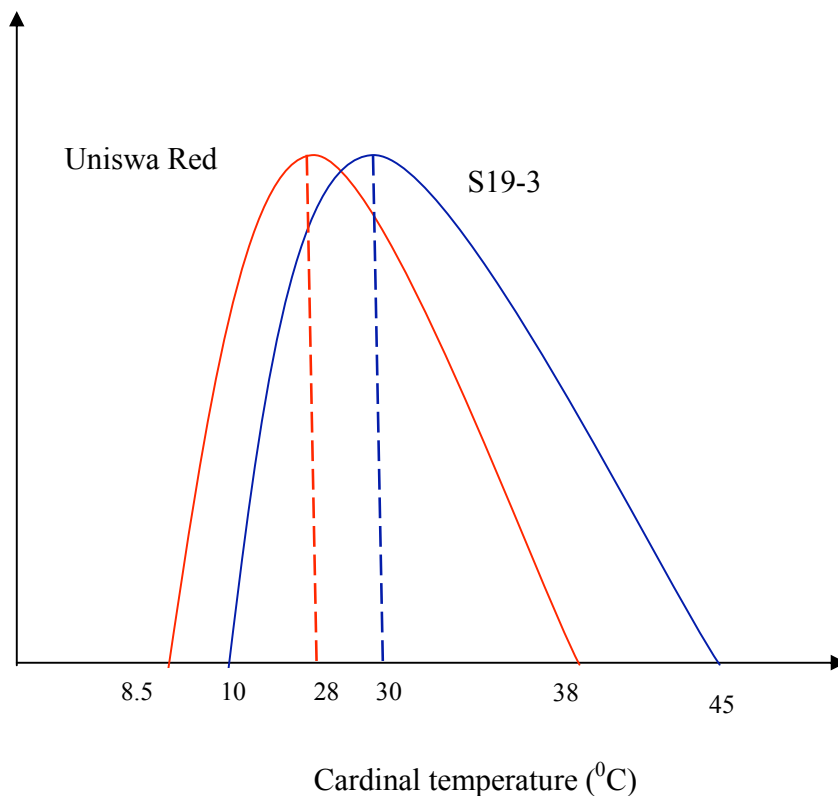


Figure 8.1. The empirical representation of cardinal temperature for Uniswa Red and S19-3.

4. The weakest link in BAMGRO is limited information to parameterise root and soil water module. Therefore it is useful to re-calibrate the model with, β (parameter describing root distribution- Chapter 7), variation of σ (specific root weight (g km^{-1})) during the growth cycle and k_w ('resource capture coefficient' cm^2) as explained in King et al. (2003). Especially resource capture coefficient- k_w can be estimated by fitting the proportional water uptake data vs root length density (L_v) as explained in Figure 8.2.

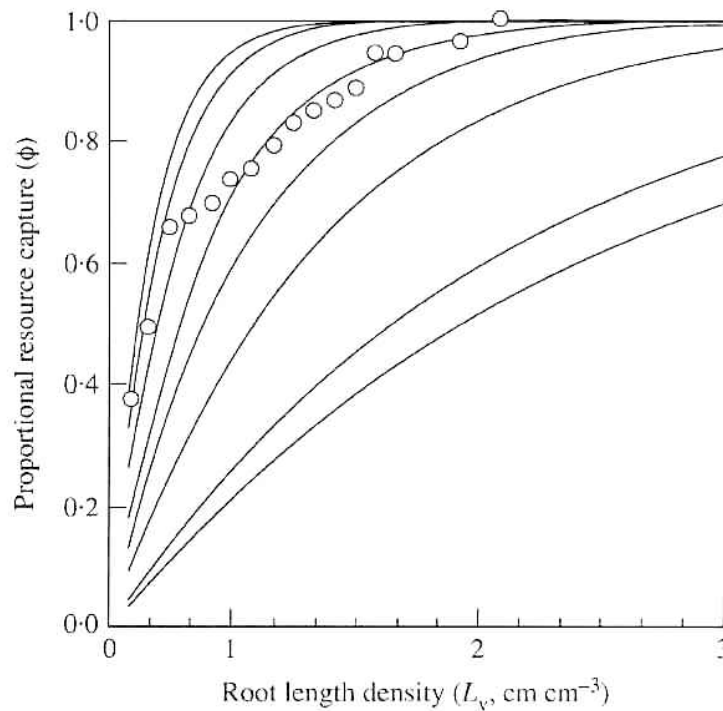


Figure 8.2. Proportional water uptake in relation to L_v . Each curve explains the different k_w from left to right $k_w = 5, 4, 3, 2, 1.5, 1, 0.5$ and 0.4 cm^2 respectively. The data points are for water capture by barley relative to the total amount of available soil moisture in the soil and L_v measured at anthesis (Gregory and Brown, 1989; King et al., 2003). As per details above, new data sets for bambara groundnut can be used to fit the above curves to estimate the k_w .

5. BAMGRO can be used as the basis for evaluating the effect of genetic variability on physiological traits. Ultimately it would be very useful to know how and what intra-landrace genetic viability contributes to each physiological trait. This model would be able to derive a result which estimates the required amount of genetic ‘width’ data to optimally inform the physiological data, for a number of scenarios. The problem statement for this has been already addressed at the event of Mathematics in Plant Sciences Study Group (<http://cpib.info/study2008/programme.shtml>).

8.8 CONCLUSIONS

A crop simulation model (BAMGRO) for an underutilised crop bambara groundnut (*Vigna subterranea* (L.) Verdc.) was developed, calibrated and validated against glasshouse (TCRU-University of Nottingham, UK) and field sites in Botswana and Swaziland and details are explained in former Chapters (1-7).

The novel approach in simulating daily rate of leaf production by means of a Gaussian function successfully simulated the canopy development of bambara groundnut landraces under abiotic stress and in varying photoperiodic levels. The daily rate of dry matter production considers the most limiting factor on growth as radiation and soil moisture by means of light limited growth (*LLG*) and water limited growth (*WLG*). The produced dry matter is partitioned among various parts within the plant considering the phenological stage and the drought stress. BAMGRO-soil water balance follows the feature of a wheat model with very simple functions.

Model validation results for canopy development, dry matter production, yield formation for a four tested landraces (Uniswa Red, S19-3, DipC and OM1) are in good agreement with measured values in glasshouse conditions in Nottingham, UK and field sites in Swaziland. Overall model validation results for yield are poorly correlated with measured values for Botswana field sites perhaps due to landrace variability. The evaluation of BAMGRO-soil water module by means of available soil water as the only source of data revealed that it was overestimated for glasshouse soil while better a correlation was reported for Botswana soil.

BIBLIOGRAPHY

- ADIKU, S. G. K., RENGGER, M., WESSOLEK, G., FACKLAM, M. and HECHT-
BUCHOLTZ, C. (2001) Simulation and dry matter production and seed
yield of common beans under varying soil water and salinity conditions.
Agricultural Water Management, **47**, 55-68.
- ANWAR, R. M., MCKENZIE, B. A. and HILL, G. D. (2003) Water-use
efficiency and the effect of water deficits on crop growth and yield of Kabuli
chickpea (*Cicer arietinum* L.) in a cool-temperate sub humid climate.
Journal of Agricultural Science, **141**, 285-301.
- AZAM-ALI, S. N. and SQUIRE, G. R. (2002) *Principles of Tropical Agronomy*,
Wallingford, UK: CAB International
- AZAM-ALI, S. N., AGUILAR-MANJARREZ, J. and BANNAYAN-AVVAL, M.
(2001) A global mapping system for bambara groundnut production. *Food
and Agriculture Organization of the United Nations*. Rome.
- BANNAYAN, M. (2001) BAMnut: a crop simulation model for bambara
groundnut. *Agricultural Sciences and Technology*, **15**, 101-110.
- BANNAYAN, M. and CROUT, N. M. J. (1999) A stochastic modeling approach
of real time forecasting of winter wheat yield. *Field Crops Research*, **62**, 85-
95.
- BASU, S., ROBERTS, J. A., DAVEY, M. R., AZAM-ALI, S. N. and MITHEN,
R. F. (2003) Towards genetic linkage mapping in bambara groundnut (*Vigna
subterranea* (L) Verdc.) In: *Proceedings of the International bambara
groundnut Symposium*. Botswana College of Agriculture, Botswana.
- BERCHIE, J. N. (1996) Light use and dry matter production of bambara
groundnut landraces in relation to soil moisture. *Department of Agriculture
and Horticulture*. Sutton Bonington Campus, University of Nottingham, UK.
- BONNET, G. D. (1998). Rate of leaf appearance in sugarcane, including a
comparison of range of varieties. *Australian Journal of Plant Physiology*. **25**,
829-834.
- BOOTE, K. J., JONES, J. W. and PICKERING, N. B. (1996) Potential uses and
limitations of crop models. *Agronomy Journal*, **88**, 704-716.
- BOOTE, K. J., JONES, J. W., HOOGENBOOM, G., WILKERSON, G. G. and
JAGTAP, S. S. (1989) PNUTGRO V1.02, Peanut crop growth simulation
model User's guide. *Florida Agricultural Experimental Station Journal*,
8420.
- BOOTE, K. J., JONES, J.W. and PICKERING, N. B. (1996) Potential uses and
limitations in crop models. *Agronomy Journal*, **88**, 704-716.

- BOOTE, K. J., MINGUEZ, M. I. and SAU, F. (2002a) Adapting the CROPGRO legume model to simulate growth of Faba bean. *Agronomy Journal*, **94**, 743-756.
- BOUTENG, C. O. (2003) Photosynthesis of 3 Bambara Groundnut (*Vigna subterranea* (L.) Verdc.) landraces in response to soil moisture stress. *School of Biosciences, Sutton Bonington Campus. University of Nottingham*.
- BRADLEY, R. G. and CROUT, N. M. J. (1993) The PARCH model. University of Nottingham, Nottingham, UK.
- BRINK, M. (1997) Rates of progress towards flowering and podding in bambara groundnut (*Vigna subterranea*) as a function of temperature and photoperiod. *Annals of Botany*, **80**, 505-513.
- BROUGH, S. H. and AZAM-ALI, S. N. (1992) The effect of soil moisture on the proximate composition of bambara groundnut (*Vigna subterranea* (L) Verdc.). *Journal of Science of Food and Agriculture*, **60**, 197-203.
- COLLINSON, S. T. (1996a) The bambara groundnut PARCH model. *Proceedings of the International Bambara Groundnut Symposium*. University of Nottingham, UK.
- COLLINSON, S. T., AZAM-ALI, S. N., CHAVULA, K. M. and HODSON, D. A. (1996) Growth, development and yield of bambara groundnut (*Vigna subterranea*) in response to soil moisture. *Journal of Agricultural Sciences (Cambridge)*, **126**, 307-318.
- COLLINSON, S. T., BERTCHIE, J. and AZAM-ALI, S. N. (1999) The effect of soil moisture on light interception and conversion coefficient for three landraces of bambara groundnut (*Vigna subterranea*). *Journal of Agricultural Sciences (Cambridge)*, **133**, 151-157.
- COLLINSON, S. T., CLAWSON, E. J., AZAM-ALI, S. N. and BLACK, C. R. (1997) Effect of soil moisture deficits on the water relations of bambara groundnut (*Vigna subterranea* (L) Verdc.). *Journal of Experimental Botany*, **48**, 877-884.
- COLLINSON, S. T., SIBUGA, K. P., TARIMO, A. J. P. and AZAM-ALI, S. N. (2000) Influence of sowing date on the growth and yield of bambara groundnut landraces in Tanzania. *Experimental Agriculture*, **36**, 1-13.
- CORNELISSEN, R. L. E. J. (2005) Modelling variation in the physiology of bambara groundnut (*Vigna subterranea* (L) Verdc.) School of Biosciences. Sutton Bonington Campus, University of Nottingham, UK.
- CRAUFURD, P. Q. and WHEELER, T. R. (1999) Effect of drought and plant density on radiation interception, radiation use efficiency and partitioning of dry matter to seeds in cowpea. *Experimental Agriculture*, **35**, 29-38.
- DE COSTA, W. A. J. M. and SHANMUGATHASAN, K. N. (2002) Physiology of yield determination of soybean (*Glycine max* (L.) under different irrigation

- regimes in the sub-humid zone of Sri Lanka. *Field Crops Research*, **75**, 23-35.
- FERRIS, R., ELLIS, R. H., WHEELER, T. R. and HADLEY, P. (1998) Effect of high temperature stress at anthesis on grain yield and biomass of field grown crops of wheat. *Annals of Botany*, **82**, 631-639.
- FLESHIER, D. H. and TIMLIN, D. (2006) Modeling expansion of individual leaves in potato canopy. *Agricultural and Forest Meteorology*, **139**, 84-93.
- FLOHR, M. L., WILLIAM, J. H. and LENZ, F. (1990) The effect of photoperiod on the reproductive development of a photoperiod sensitive groundnut (*Arachis hypogaea* L.). *Experimental Agriculture*, **26**, 397-406.
- GALE, M. R. and GRIGAL, D. F. (1987) Vertical root distribution of northern tree species in relation to successional status. *Canadian Journal of Forest Research*, **17**, 829-834.
- GREGORY, P. J. and BROWN, S. C. (1989) Root growth. Water use and yield of crops in dry environments: What characteristics are desirable? *Aspects of Applied Biology*, **22**, 235-243.
- GRIMM, S. S., JONES, J.W., BOOTE, K.J. and HERZOG, D. C (1994) Modelling the occurrence of reproductive stages after flowering for four soya bean cultivars. *Agronomy Journal*, **86**, 31-38.
- HAMBLIN, A. and TENNANT, D. (1987) Root length density and water uptake in cereals and grain legumes: How well are they correlated? *Australian Journal of Agricultural Research*, **38**, 513-527.
- HAMMER, G. L., SINCLAIR, T. R., BOOTE, K. J., WRIGHT, G. C., MEINKE, H. and BELL, M. J. (1995) A peanut simulation model: I. Model development and testing. *Agronomy Journal*, **87**, 1085-1093.
- HARRIS, D. and AZAM-ALI, S. N. (1993) Implication of day length sensitivity in bambara groundnut (*Vigna subterranea*) for production in Botswana. *Journal of Agricultural Sciences (Cambridge)*, **120**, 75-78
- HIRT, H. and SHINOZAKI, K. (2004) Plant responses to abiotic stress. **4**, 300pp.
- HUSAIN, M. M., REID, J. B., OTHMAN, H. and GALLAGHER, J. N. (1990) Growth and water use of faba beans (*Vicia faba*) in a sub humid climate 1. Root and shoot adaptation to drought stress. *Field Crops Research*, **23**, 1-17.
- ISMAIL, A. M. and HALL, A. E. (1999) Reproductive stage heat tolerance, leaf membrane thermostability and plant morphology in cowpea. *Crop Science*, **39**, 1762-1768.
- JONES, C. A. and KINIRY, J. R. (1986) *CERES-Maize: A simulation model of maize growth and development*. , College Station, Texas and M University Press.
- JONES, H. G. (1992) *Plants and microclimate: a quantitative approach to environmental plant physiology*. Cambridge, Cambridge University Press.

- JONES, J. W., HOOGENBOOM, G., PORTER, C. H., BOOTE, K. J., BATCHELOR, W. D., HUNT, L. A., WILKENS, P. W., SINGH, U., GIJSMAN, A. J. and RITCHIE, J. T. (2003) The DSSAT cropping system model. *European Journal of Agronomy*, **18**, 235-265.
- KARIKARI, S. K., SEBOLAI, B. and MUNTHALI, D. C. (1996) Field studies of bambara groundnut in Botswana. *Proceedings of the international bambara groundnut Symposium*. University of Nottingham, UK.
- KIJOJI, A. A. (2003) Response of 3 Bambara Groundnut (*Vigna subterranea* (L.) Verdc.) landraces to soil moisture stress. School of Biosciences. Sutton Bonington Campus, University of Nottingham, UK.
- KING, J., GRAY, A., BRADELY, R. G., BINHAM, I., FOILKS, J., GREGORY, P. and ROBINSON, D. (2003) Modelling cereal root system for water and nitrogen capture: Towards an economic optimum. *Annals of Botany*, **91**, 383-390.
- KINIRY, J. R., LANDIVAR, J. A., WITT, M., GERIK, T. J., CAVERO, J. and WADE, L. J. (1998) Radiation use efficiency response to vapour pressure deficit for maize and sorghum. *Field Crops Research*, **56**, 265-270.
- KOCABAS, Z., GRAIGON, J. and AZAM-ALI, S. N. (1999) The germination response of bambara groundnut (*Vigna subterranea* (L.) Verdc.) to temperature. *Seed Science and Technology*, **27**, 303-313.
- LEPORT, L., TURNER, N. C., FRENCH, R. J., BARR, M. D., DUDA, R., DAVIS, S. L., TENNANT, D. and SIDIQUE, K. H. M. (1999) Physiological responses of chickpea genotypes to terminal drought in a Mediterranean-type environment. *European Journal of Agronomy*, **11**, 279-291.
- LINNEMANN, A. R. (1991a) Preliminary observations on photoperiod regulation of phenological development in bambara groundnut (*Vigna subterranea*). *Field Crop research*, **26**, 295-304.
- LINNEMANN, A. R. (1991b) Influence of photoperiod on development of bambara groundnut (*Vigna subterranea* (L.) Verdc.). *Acta Botanica Neerlandica*, **40**, 374.
- LINNEMANN, A. R. (1993) Phenological development in bambara groundnut (*Vigna subterranea* (L.) Verdc.) at constant exposure to photoperiods of 10 to 16 h. *Annals of Botany*, **71**, 445-452.
- LINNEMANN, A. R. and AZAM-ALI, S. N. (1993) Bambara groundnut (*Vigna subterranea*). In: *Underutilised Crops Pulses and Vegetables*, London, Chapman and Hall.
- LINNEMANN, A. R. and CRAUFURD, P. Q. (1994) Effects of temperature and photoperiod on phenological development in three genotypes of bambara groundnut (*Vigna subterranea*). *Annals of Botany*, **74**, 675-681.
- MANSCHADI, A. M., AUERBORN, J., STUTZEL, H., GOBEL, W. and SAXENA, M. C. (1998) Simulation of faba bean (*Vicia faba* L.) root system

- development under Mediterranean conditions. *European Journal of Agronomy*, **9**, 259-272.
- MARCELIS, L. F. M. (1993a) Simulation of biomass allocation in greenhouse crops, a review. *Acta Horticulture*, **54**, 107-121.
- MARCELIS, L. F. M. (1994) A simulation model for dry matter partitioning in cucumber. *Annals of Botany*, **74**, 43-52.
- MASSAWE, F. J., AZAM-ALI, S. N. and ROBERTS, J. A. (2003) The impact of temperature on leaf appearance in bambara groundnut landraces. *Crop Science*, **43**, 1375-1379.
- MATTHEWS, R. B. and STEPHENS, W. (1998a) CUPPA TEA: A simulation model describing seasonal yield variation and potential production of tea. 1. Shoot development and extension. *Experimental Agriculture*, **34**, 345-367.
- MATTHEWS, R. B. (2006) PALM: An agent-based spatial model of livelihood generation and resource flows in rural households and their environment. *Ecological modelling*, **194**, 329-343.
- MATTHEWS, R. B. and HUNT, L. A. (1994) GUMCAS: A model describing the growth of cassava (*Manihot esculenta* L. Crantz). *Field Crop Research*, **36**, 69-84.
- MATSUI, T., OMASA, K. and HORIE, T. (2001) The difference in sterility due to high temperature during the flowering period among japonica rice varieties. *Plant Production Science*, **4**, 90-93.
- MEISNER, C. A. and KARNOK, K. J. (1992) Peanut root response to drought stress. *Agronomy Journal*, **84**, 159-165.
- MONTEITH, J. L. (1996) The quest for balance in crop modelling. *Agronomy Journal*, **88**, 695-697.
- MONTEITH, J. L., MARSHALL, B., SAFFELL, R. A., CLARKE, D., GALLAGHER, N., GREGORY, P. J., ONG, C. K., SQUIRE, G. R. and TERRY, A. (1983) Environmental control of a glasshouse suit for crop physiology. *Journal of Experimental Botany*, **34**, 309, 321.
- MONTEITH, J.L. (1986) How do crops manipulate water supply and demand? Philosophical Transactions of the Royal Society of London Series A-Mathematical Physical and Engineering Sciences, **316**, 245-259.
- MUCHOW, R. C. and SINCLAIR, T. R. (1994) Nitrogen response of leaf photosynthesis and canopy radiation use efficiency in field grown maize and sorghum, *Crop Science*, **34**, 721-727.
- MWALE, S. S. (2005) Resource use efficiency of bambara groundnut landraces in response to soil water. PhD thesis, School of Biosciences. Sutton Bonington Campus, University of Nottingham, UK.
- MWALE, S. S., AZAM-ALI, S. N. and MASSAWE, F. J. (2007a) Growth and development of bambara groundnut (*Vigna subterranea*) in response to soil

- moisture 1. Dry matter and yield. *European Journal of Agronomy*, **26**, 345-353.
- MWALE, S. S., AZAM-ALI, S. N. and MASSAWE, F. J. (2007b) Growth and development of bambara groundnut (*Vigna subterranea*) in response to soil moisture 2. Resource capture and conversion. *European Journal of Agronomy*, **26**, 354-362.
- MWANAMWENGE, J., LOSS, S. P. and SIDDIQUE, K. H. M., COCKS, P. S. (1999) Effect of water stress during floral initiation, flowering and podding on the growth and yield of faba bean (*Vicia faba* L.). *European Journal of Agronomy*, **11**, 1-11.
- NASH, J.E. and SUTCLIFFE, J.V. (1970) River flow forecasting through conceptual models. Part 1- a discussion of principles, *Journal of Hydrology*, **227**, 282-290.
- ONIMAWO, I. A., MOMOH, A. H. and USMAN, A. (1998) Proximate composition and functional properties of four cultivars of bambara groundnut (*Vigna subterranea*). *Plant Foods for Human Nutrition*, **53**, 153-158.
- PAGADALA, V. V. P., CRAUFURD, P. Q., SUMMERFIELD, R. J. and WHEELER, T. R. (2000) Effect of short episodes of heat stress on flower production and fruit-set of groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany*, **51**(345), 777-784.
- PANNU, R. K. and SINGH, D. P. (1993) Effect of irrigation on water use, water-use efficiency, growth and yield of mungbean. *Field Crops Research*, **31**, 87-100.
- PASQUET, R. S., SCHWEDES, S. and GEPTPS, P. (1999) Isosyme diversity in bambara groundnut. *Crop Science*, **39**, 1228-1236.
- PEARCE, E. A. and SMITH, C. G. (1998) Fodor's world weather guide, Random House, New York.
- PRIESTLY, C. H. B. and TAYLOR, R. J. (1972) On the assessment of surface heat flux and evaporation using large scale parameters. *Mon. Weather Review*, **100**, 81-92.
- RANGANATHAN, R., CHAUHAN, Y. S., FLOWER, D. J., ROBERTSON, M. J., SANETRA, C. and SILIM, S. N. (2001) Predicting growth and development of pigeonpea: leaf area development. *Field Crops Research*, **69**, 163-172.
- RAO, R. C. N., SIMMONDS, L. P., AZAM-ALI, S. N. And WILLIAMS, J.H. (1989) Population growth and water-use of groundnut maintained on stored water 1. Root and shoot growth. *Experimental Agriculture*, **25**, 51-61.
- RITCHIE, J. T. (1972) Model for predicting evaporation from a row crop with incomplete cover. *Water Resource Research*, **8**, 1204-1213.

- ROBERTSON, M. J., FUKAI, S., LUDLOW, M. M., and HAMMER, G. L. (1993a) Water extraction by grain-sorghum in a sub humid environment. 1. Analysis of the water extraction patters. *Field Crops Research*, **33**, 99-112.
- ROBERTSON, M. J., CARBERRY, P. S., CHAUHAN, Y. S., RANGANATHAN, R. and O'LEARY, G. J. (2001) Predicting growth and development of pigeonpea: a simulation model. *Field Crops Research*, **71**, 195-210.
- ROBERTSON, M. J., CARBERRY, P. S., HUTH, N. I., TURPIN, J. E., PROBERT, M. E., POULTON, P. L., BELL, M., WRIGHT, G. C., YEATES, J. S. and BRINSMEAD, R. B. (2002) Simulation of growth and development of diverse legume species in APSIM. *Australian Journal of Agricultural Research*, **53**, 429-446.
- ROOSE, T. and FOWLER, A. C. (2004) A model for water uptake by plant roots. *Journal of Theoretical Biology*, **228**, 155-171.
- SESSAY, A. and YARMAH, A. (1996) Filed studies of bambara groundnut in Sierra Leone. *Proceedings of the international bambara groundnut Symposium*. University of Nottingham, UK.
- SHAMUDZARIRA, Z. (1996) Water use and dry matter production in Sorghum and Bambara groundnut (*Vigna subterranea* (L.) Verdc.) School of Biosciences. Sutton Bonington Campus, University of Nottingham, UK.
- SINCLAIR, T. R. (1986) Water and nitrogen limitations in soybean grain production: I. Model development. *Field Crops Research*, **15**, 125-141.
- SINCLAIR, T. R. and SELIGMAN, N. G. (1996) Crop modelling: From infancy to maturity. *Agronomy Journal*, **88**, 698-704.
- SINGH, P. and VIRMANI, S. M. (1996) Modelling growth and yield of chickpea (*Cicer arietinum* L.). *Filed Crop research*, **46**, 41-59.
- SOLTANI, A., ROBERTSON, M. J., RAHEMI-KARIZAKI, A., POORREZA, J. and ZAREI, H. (2006) Modelling biomass accumulation and portioning in chickpea (*Cicer arietinum* L.). *Journal of Agronomy and Crop Science*, **192**, 379-389.
- SQUIRE, G. R. (1990) The physiology of tropical crop production. *CAB International, Wallingford, UK* 236pp.
- THOMAS, FUKAI, S. and HAMMER, G. L. (1995) Growth and yield response of barley and chickpea to water stress under 3 environments in Southeast queensland 2. Root growth and soil water extraction pattern. *Australian Journal of Agricultural Research*, **46**, 35-48.
- THORNLEY, J. H. M. and JOHNSON, J. R. (1990) Plant and crop modelling. A mathematical approach to plant and crop physiology. Clarendon Press, Oxford.
- TINGEM, M., RIVINGTON, M., AZAM-ALI, S. N. and COLLS, J. J. (2008) The impacts of climate change on crop production in Cameroon. *Climate Research*, **36**, 65-77.

- TURMAN, P. C., WIEBOLD, W. J., WRATHER, J. A and TRACY, P. W. (1995) Cultivar and planting date effects on soybean root growth. *Plant and Soil*, **176**, 235-241.
- TURNER, N. C. (1997) Further, progress in crop water relations. *Advances in Agronomy*, **58**, 293-338.
- UHERA, G. and TSUJI, G. Y. (1993) *The IBSNAT project* Dordrecht, Kluwer.
- WAINWRIGHT, J. and MULLIGAN, M. (2002) Measurement of model goodness - of - fit in Environmental Modelling, Department of Geography, King's College London.
- WHEELER, T. R., KEATINGE, J. D. H, ELLIS, R. H., SUMMERFIELD, R. J. and CRAUFURD, P. Q. (1999) Modelling the effect of temperature on the rates of seedling emergence and leaf appearance in legume cover crops. *Experimental Agriculture*, **35**, 327-344.
- WHEELER, T. R., CRAUFURD, P. Q., ELLIS, R. H., PORTER, J. R. and VARA PRASAD, P. V. (2000) Temperature variability and the yields of annual crops. *Agriculture, Ecosystem and Environment*, **82**, 159-167.
- WILKERSON, G. G., JONES, G. W., BOOTE, K. J. and MISHOE, J. W. (1985) *SOYGRO V5.0.*, Agricultural Engineering Department, University of Florida.

APPENDIX 1. Codes for BAMGRO model used in Model Maker 3.0

```

parameter: t    151    0
Main
variable: BAMGROmain Unconditional
BAMGROmain = 0
parameter: BD  1.4    0
Cropgrowthmodule
variable: Ad Conditional Global
Ad =
  THERMALTIME/(Topt-Tbase)*(1/DLfac) by default
independent event: Canopydevelopment Active Reset
Period: 1
0
Actions:
rate=(a*exp(-0.5*((TT-b/(c))^2))*thermaltime*DLfac;

If (PHENO<P0){
rate=0
}
compartment: DeadLwt Unconditional Global
dDeadLwt/dt = +F1
Initial Value = 0.0
variable: Densityfac Unconditional
Densityfac = TCRUdensity/Density
variable: Drymatter Unconditional Universal
Drymatter = (MIN(LLG,WLG))
define value: F_Leaf Unconditional
F_Leaf = 0
define value: F_Pod Unconditional
F_Pod = 0
define value: F_Root Unconditional
F_Root = 0
define value: F_Stem Conditional Global
F_Stem =
  0 by default
flow: F1 Unconditional
Flow from LEAFW to DeadLwt
F1 = KS2* LEAFW
variable: Grainfill Conditional Universal
Grainfill =
  grainconstant*Ks3 by default
compartment: Grainwt Unconditional
dGrainwt/dt = GrainWtrate
Initial Value = 0
define value: GrainWtrate Unconditional
GrainWtrate = 0
variable: Ks1 Conditional Universal
Ks1 =
  Min(WSTRESS,1) for Tmean>Topt
  Min(TSTRESS,WSTRESS) for Tmean<Topt

```

Min(TSTRESS,WSTRESS) by default
 variable: KS2 Conditional
 KS2 =
 Max(SenL,SenW,SenT,SenPhy) by default
 variable: Ks3 Conditional
 Ks3 =
 WSTRESS by default
 variable: LAI Unconditional Universal
 $LAI = LEAFAREA * DENSITY / 10000$
 variable: LEAFAREA Conditional
 LEAFAREA =
 0.001 for PHENO<0
 Leafnumber*LA1 by default
 compartment: LEAFnumber Conditional Universal
 $dLEAFnumber/dt =$
 0 for pheno<P0
 (rate)-(Leafnumber*Ks2) for pheno>(p0+p1)
 rate by default
 Initial Value = 6
 compartment: LEAFW Conditional Global
 $dLEAFW/dt =$
 (Drymatter*F_Leaf)-(F1+(LEAFW*0)) by default
 Initial Value = 0.0
 variable: LEAFWtotal Unconditional Global
 $LEAFWtotal = LEAFW + DeadLWT$
 variable: LLG Conditional Universal
 LLG =
 (0.5*SRAD*RUE*(1-EXP(-KEXT*LAI))) by default
 variable: MaxP Conditional
 MaxP =
 MaxpodN/2 for Tmean<Topt and WSTRESS<1
 MaxpodN*TSTRESS for Tmean>Topt
 MaxpodN by default
 independent event: PARTITIONevent Active Reset
 Period: 1
 0
 Actions:
 $F_Leaf = ((-0.00003 * TT) + 0.70) * Ks3;$
 If(Tmean<Topt){
 $F_Leaf = ((-0.0001 * TT) + 0.70) * Ks3$
 }
 $F_Stem = 0.26;$
 If (PHENO<(P0+P3+P4)){
 $F_Root = 1 - (F_Leaf + F_Stem)$
 }
 If (PHENO<(P0+P3+P4)){
 $F_Pod = 0$
 }
 If (PHENO>(P0+P3+P4)){
 $F_Root = (F_Leaf + F_Stem) * 0.04$
 }

```

If (PHENO>(P0+P3+P4)){
F_Pod=1-(F_Leaf+F_Stem+F_root)
}
If(TT>b){
PodNrate=(1/rate)*thermaltime
}else{
PodNrate=0
}

If(PodN>Maxp){
PodNrate=0
}

If (PHENO>(P0+P3+P4)){
Relocation=Grainfill-((Drymatter*F_pod)/(PodN))
}else{
relocation=0
}

If (Grainwt>maxsize){
Relocation=0
}

if (PodNrate>0){
GrainWtrate=((Drymatter*F_pod)/(PodN))+relocation
}

Total=F_Root+F_Leaf+F_Stem+F_Pod;

F_Root=F_Root/Total;
F_Leaf=F_Leaf/Total;
F_Stem=F_Stem/Total;
F_Pod=F_Pod/Total;

Totalcheck=F_Root+F_Leaf+F_Stem+F_Pod;
compartment: PHENO Unconditional Universal
dPHENO/dt = Ad
Initial Value = 0
compartment: podN Conditional
dpodN/dt =
PodNrate by default
Initial Value = 0.001
define value: PodNrate Unconditional
PodNrate = 0
variable: PW Unconditional Global
PW = PodN*Grainwt
define value: rate Unconditional Global
rate = 0
define value: Relocation Unconditional
Relocation = 0
variable: ROOTWT Unconditional Universal

```

ROOTWT = Drymatter*F_Root
 compartment: RW Conditional Universal
 dRW/dt =
 SeedRelocation for PHENO<=P0
 Drymatter*F_Root for PHENO>P0
 Drymatter*F_Root by default
 Initial Value = 0.0001
 variable: SeedRelocation Conditional
 SeedRelocation =
 0 for PHENO>P0
 Density*SeedW*FRs for PHENO<=P0
 Density*SeedW*FRs by default
 variable: SENL Conditional
 SENL =
 MAX(MIN(0.15*(LAI-5),1),0) for Tmean>Topt
 MAX(MIN(0.03*(LAI-3),1),0) by default
 variable: SENphy Conditional
 SENphy =
 0.008 for Tmean>Topt and PHENO>(P0+P1+P2)
 .003 for PHENO>(P0+P1+P2)
 0.003 by default
 variable: SENT Conditional
 SENT =
 MAX(MIN(((TSTRESS)*0.001),1),0) for Tmean<Topt
 MAX(MIN(((TSTRESS)*0.01),1),0) for Tmean>Topt and WSTRESS<1
 MAX(MIN(((TSTRESS)*0.001),1),0) for Tmean>Topt
 0 by default
 variable: SENW Conditional
 SENW =
 MAX(MIN(((WSTRESS)*0.02),1),0) for WSTRESS<1 and Tmean<=Topt
 MAX(MIN(((WSTRESS)*0.07),1),0) for WSTRESS<1 and Tmean>Topt
 0 by default
 compartment: STEMW Conditional Global
 dSTEMW/dt =
 0 for Pheno<P0
 Drymatter*F_Stem by default
 Initial Value = 0.0
 variable: TCRUdensity Unconditional
 TCRUdensity = 14
 variable: TDM Unconditional
 TDM = LEAFW+DEADLWT+STEMW+PW
 define value: Total Unconditional
 Total = 0
 define value: TotalCheck Unconditional
 TotalCheck = 0
 Landracecoefficients
 variable: A Unconditional Universal
 A = A_data
 variable: B Unconditional Universal
 B = B_data
 variable: beta1 Unconditional Universal

beta1 = beta1_data
 variable: beta2 Unconditional Universal
 beta2 = beta2_data
 variable: c Unconditional Universal
 c = c_data
 variable: Daylength Unconditional Universal
 Daylength = Daylength_data
 variable: Density Unconditional Universal
 Density = Density_data
 variable: FRs Unconditional Universal
 FRs = FRs_data
 variable: Grainconstant Unconditional Universal
 Grainconstant = Grainconstant_data
 variable: KEXT Unconditional Universal
 KEXT = KEXT_data
 variable: LA1 Unconditional Universal
 LA1 = LA1_data
 lookup table: LandraceCoefficients
 Landraces Control
 Tbase_data Controlled by: Landraces Universal
 Linear interpolation
 Topt_data Controlled by: Landraces Universal
 Linear interpolation
 Thigh_data Controlled by: Landraces Universal
 Linear interpolation
 P0_data Controlled by: Landraces Universal
 Linear interpolation
 P1_data Controlled by: Landraces Universal
 Linear interpolation
 P2_data Controlled by: Landraces Universal
 Linear interpolation
 P20_data Controlled by: Landraces Universal
 Linear interpolation
 P2R_data Controlled by: Landraces Universal
 Linear interpolation
 P3_data Controlled by: Landraces Universal
 Linear interpolation
 P4_data Controlled by: Landraces Universal
 Linear interpolation
 P5_data Controlled by: Landraces Universal
 Linear interpolation
 P6_data Controlled by: Landraces Universal
 Linear interpolation
 KEXT_data Controlled by: Landraces Universal
 Linear interpolation
 RUE_data Controlled by: Landraces Universal
 Linear interpolation
 LA1_data Controlled by: Landraces Universal
 Linear interpolation
 daylength_data Controlled by: Landraces Universal
 Linear interpolation

density_data Controlled by: Landraces Universal
 Linear interpolation
 a_data Controlled by: Landraces Universal
 Linear interpolation
 b_data Controlled by: Landraces Universal
 Linear interpolation
 c_data Controlled by: Landraces Universal
 Linear interpolation
 grainconstant_data Controlled by: Landraces Universal
 Linear interpolation
 MAXsize_data Controlled by: Landraces Universal
 Linear interpolation
 MAXPodN_data Controlled by: Landraces Universal
 Linear interpolation
 SeedW_data Controlled by: Landraces Universal
 Linear interpolation
 FRs_data Controlled by: Landraces
 Linear interpolation
 beta2_data Controlled by: Landraces Universal
 Linear interpolation
 beta1_data Controlled by: Landraces Universal
 Linear interpolation
 TE_data Controlled by: Landraces
 Linear interpolation
 SRW_data Controlled by: Landraces
 Linear interpolation
 TLower_data Controlled by: Landraces
 Linear interpolation
 Maxrate_data Controlled by: Landraces
 Linear interpolation
 TUpper_data Controlled by: Landraces
 Linear interpolation
 define value: Landraces Unconditional
 Landraces = 1
 variable: MAXPODN Unconditional Universal
 MAXPODN = MAXpodN_data
 variable: Maxrate Unconditional Universal
 Maxrate = Maxrate_data
 variable: MAXsize Unconditional Universal
 MAXsize = MAXsize_data
 variable: P0 Unconditional Universal
 P0 = P0_data
 variable: P1 Unconditional Universal
 P1 = P1_data
 variable: P2 Unconditional Universal
 P2 = P2_data
 variable: P20 Unconditional Universal
 P20 = P20_data
 variable: P2R Unconditional Universal
 P2R = P2R_data
 variable: P3 Unconditional Universal

P3 = P3_data
 variable: P4 Unconditional Universal
 P4 = P4_data
 variable: P5 Unconditional Universal
 P5 = P5_data
 variable: P6 Unconditional Universal
 P6 = P6_data
 variable: RUE Unconditional Universal
 RUE = RUE_data
 variable: SeedW Unconditional Universal
 SeedW = SeedW_data
 variable: SRW Unconditional Universal
 SRW = SRW_data
 variable: Tbase Unconditional Universal
 Tbase = Tbase_data
 variable: TE Unconditional Universal
 TE = TE_data
 variable: Thigh Unconditional Universal
 Thigh = Thigh_data
 variable: TLowerthreshhold Unconditional Universal
 TLowerthreshhold = TLower_data
 variable: Topt Unconditional Universal
 Topt = Topt_data
 variable: TUpperthreshhold Unconditional Universal
 TUpperthreshhold = TUpper_data
 Photoperiodmodule
 variable: DLfac Conditional Universal
 DLfac =
 1 for DL<=12
 (0.25*DL) for DL>12 and Pheno>P0
 1 by default
 lookup file: Photoperiod C:\BAMGRO\Weather files\Weather 2007\Photoperiod-TCRU.txt
 t Control
 DL Controlled by: t
 Linear interpolation
 SoilWatermodule
 variable: beta Unconditional Global
 beta = beta1*(TT^beta2)
 variable: Cover Unconditional
 Cover = (1-EXP(-KEXT*LAI))
 parameter: deltaZ1 100 0
 parameter: deltaZ2 900 0
 parameter: deltaZ3 500 0
 flow: DR1 Unconditional
 Flow from WATER1 to WATER2
 DR1 = max((WATER1-FClayers),0)
 flow: DR10 Unconditional
 Flow from WATER10 to WATER11
 DR10 = max((WATER10-FClayers),0)
 flow: DR11 Unconditional

Flow from WATER11 to WATER12
 $DR11 = \max(\text{WATER11-FClayers}, 0)$
 flow: DR12 Unconditional
 Flow from WATER12 to WATER13
 $DR12 = \max((\text{WATER12-FClayers}), 0)$
 flow: DR13 Unconditional
 Flow from WATER13 to WATER14
 $DR13 = \max((\text{WATER13-FClayers}), 0)$
 flow: DR14 Unconditional
 Flow from WATER14 to WATER15
 $DR14 = \max((\text{WATER14-FClayers}), 0)$
 flow: DR15 Unconditional
 Flow from WATER15 to SEEPAGE
 $DR15 = \max((\text{WATER15-FClayers}), 0)$
 flow: DR2 Unconditional
 Flow from WATER2 to WATER3
 $DR2 = \max((\text{WATER2-FClayers}), 0)$
 flow: DR3 Unconditional
 Flow from WATER3 to WATER4
 $DR3 = \max(\text{WATER3-FClayers}, 0)$
 flow: DR4 Unconditional
 Flow from WATER4 to WATER5
 $DR4 = \max((\text{WATER4-FClayers}), 0)$
 flow: DR5 Unconditional
 Flow from WATER5 to WATER6
 $DR5 = \max((\text{WATER5-FClayers}), 0)$
 flow: DR6 Unconditional
 Flow from WATER6 to WATER7
 $DR6 = \max((\text{WATER6-FClayers}), 0)$
 flow: DR7 Unconditional
 Flow from WATER7 to WATER8
 $DR7 = \max((\text{WATER7-FClayers}), 0)$
 flow: DR8 Unconditional
 Flow from WATER8 to WATER9
 $DR8 = \max((\text{WATER8-FClayers}), 0)$
 flow: DR9 Unconditional
 Flow from WATER9 to WATER10
 $DR9 = \max((\text{WATER9-FClayers}), 0)$
 parameter: E1 0.08 0
 parameter: E2 0.08 0
 parameter: E3 0.08 0
 variable: Evapo Unconditional
 $\text{Evapo} = \text{MAX}((\text{PotEvapo} * (\text{WATER1-PWP}) / (\text{FClayers-PWP})), 0)$
 variable: FClayers Unconditional Universal
 $\text{FClayers} = \text{FCsoil} * 100$
 variable: FCsoil Unconditional Global
 $\text{FCsoil} = 0.44 * \text{SatCapacity}$
 parameter: initialmoisture 0.2 0
 variable: LLG Unconditional Universal
 $\text{LLG} = \text{LLG}$
 variable: Lv1 Unconditional Global

$Lv1 = Z1 * (RW / \sigma)$
 variable: Lv10 Unconditional Global
 $Lv10 = (Z10 - Z9) * (RW / \sigma)$
 variable: Lv11 Unconditional Global
 $Lv11 = (Z11 - Z10) * (RW / \sigma)$
 variable: Lv12 Unconditional Global
 $Lv12 = (Z12 - Z11) * (RW / \sigma)$
 variable: Lv13 Unconditional Global
 $Lv13 = (Z13 - Z12) * (RW / \sigma)$
 variable: Lv14 Unconditional Global
 $Lv14 = (Z14 - Z13) * (RW / \sigma)$
 variable: Lv15 Unconditional Global
 $Lv15 = (Z15 - Z14) * (RW / \sigma)$
 variable: Lv2 Unconditional Global
 $Lv2 = (Z2 - Z1) * (RW / \sigma)$
 variable: Lv3 Unconditional Global
 $Lv3 = (Z3 - Z2) * (RW / \sigma)$
 variable: Lv4 Unconditional Global
 $Lv4 = (Z4 - Z3) * (RW / \sigma)$
 variable: Lv5 Unconditional Global
 $Lv5 = (Z5 - Z4) * (RW / \sigma)$
 variable: Lv6 Unconditional Global
 $Lv6 = (Z6 - Z5) * (RW / \sigma)$
 variable: Lv7 Unconditional Global
 $Lv7 = (Z7 - Z6) * (RW / \sigma)$
 variable: Lv8 Unconditional Global
 $Lv8 = (Z8 - Z7) * (RW / \sigma)$
 variable: Lv9 Unconditional Global
 $Lv9 = (Z9 - Z8) * (RW / \sigma)$
 parameter: PanE 2 0
 variable: PotEvapo Unconditional
 $PotEvapo = PanE * (1 - cover)$
 variable: PWP Unconditional Global
 $PWP = FCsoil / 4$
 variable: PWPlayers Unconditional Global
 $PWPlayers = PWP * 100$
 variable: ResourceCoeff Conditional Global
 $ResourceCoeff =$
 0.6 for $Tmean < Topt$
 2 by default
 variable: SatCapacity Unconditional
 $SatCapacity = 1 - (BD / 2.6)$
 compartment: SEEPAGE Unconditional
 $dSEEPAGE / dt = +DR15$
 Initial Value = 0.0
 variable: Sigma Conditional Global
 $Sigma =$
 $SRW * 0.8$ for $tmean < Topt$
 SRW by default
 variable: Uactual Conditional Global
 $Uactual =$

$\min(\text{LLG}/\text{WLG}, 1) * \text{Upot}$ by default
 variable: UP1 Conditional
 UP1 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot1}, 0))$ by default
 variable: UP10 Conditional
 UP10 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot10}, 0))$ by default
 variable: UP11 Conditional
 UP11 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot11}, 0))$ by default
 variable: UP12 Conditional
 UP12 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot12}, 0))$ by default
 variable: UP13 Conditional
 UP13 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot13}, 0))$ by default
 variable: UP14 Conditional
 UP14 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot14}, 0))$ by default
 variable: UP15 Conditional
 UP15 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot15}, 0))$ by default
 variable: UP2 Conditional
 UP2 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot2}, 0))$ by default
 variable: UP3 Conditional
 UP3 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot3}, 0))$ by default
 variable: UP4 Conditional
 UP4 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot4}, 0))$ by default
 variable: UP5 Conditional
 UP5 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot5}, 0))$ by default
 variable: UP6 Conditional
 UP6 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot6}, 0))$ by default
 variable: UP7 Conditional
 UP7 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot7}, 0))$ by default
 variable: UP8 Conditional
 UP8 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot8}, 0))$ by default
 variable: UP9 Conditional
 UP9 =
 $(\text{Uactual}/\text{Upot}) * (\max(\text{Upot9}, 0))$ by default
 variable: Upot Unconditional Global
 Upot = $((\max(\text{Upot1}, 0)) + (\max(\text{Upot2}, 0)) + (\max(\text{Upot3}, 0)) + (\max(\text{Upot4}, 0))$
 $+ (\max(\text{Upot5}, 0)) + (\max(\text{Upot6}, 0)) + (\max(\text{Upot7}, 0)) + (\max(\text{Upot8}, 0)) + (\max(\text{Upot9}, 0))$
 $+ (\max(\text{Upot10}, 0)) + (\max(\text{Upot11}, 0)) + (\max(\text{Upot12}, 0))$
 $+ (\max(\text{Upot13}, 0)) + (\max(\text{Upot14}, 0)) + (\max(\text{Upot15}, 0)))$

variable: Upot1 Unconditional Global

$$\text{Upot1} = (\text{WATER1-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv1})) * \text{E1}$$
 variable: Upot10 Unconditional Global

$$\text{Upot10} = (\text{WATER10-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv10})) * \text{E3}$$
 variable: Upot11 Unconditional Global

$$\text{Upot11} = (\text{WATER11-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv11})) * \text{E3}$$
 variable: Upot12 Unconditional Global

$$\text{Upot12} = (\text{WATER12-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv12})) * \text{E3}$$
 variable: Upot13 Unconditional Global

$$\text{Upot13} = (\text{WATER13-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv13})) * \text{E3}$$
 variable: Upot14 Unconditional Global

$$\text{Upot14} = (\text{WATER14-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv14})) * \text{E3}$$
 variable: Upot15 Unconditional Global

$$\text{Upot15} = (\text{WATER15-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv15})) * \text{E3}$$
 variable: Upot2 Unconditional Global

$$\text{Upot2} = (\text{WATER2-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv2})) * \text{E2}$$
 variable: Upot3 Unconditional Global

$$\text{Upot3} = (\text{WATER3-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv3})) * \text{E2}$$
 variable: Upot4 Unconditional Global

$$\text{Upot4} = (\text{WATER4-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv4})) * \text{E2}$$
 variable: Upot5 Unconditional Global

$$\text{Upot5} = (\text{WATER5-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv6})) * \text{E2}$$
 variable: Upot6 Unconditional Global

$$\text{Upot6} = (\text{WATER6-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv6})) * \text{E2}$$
 variable: Upot7 Unconditional Global

$$\text{Upot7} = (\text{WATER7-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv7})) * \text{E2}$$
 variable: Upot8 Unconditional Global

$$\text{Upot8} = (\text{WATER8-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv8})) * \text{E2}$$
 variable: Upot9 Unconditional Global

$$\text{Upot9} = (\text{WATER9-PWPlayers}) * (1 - \text{EXP}(-\text{ResourceCoeff} * \text{Lv9})) * \text{E2}$$
 variable: WATER Unconditional

$$\text{WATER} = \text{WATER1} + \text{WATER2} + \text{WATER3} + \text{WATER4} + \text{WATER5} + \text{WATER6} + \text{WATER7} + \text{WATER8} + \text{WATER9} + \text{WATER10}$$
 compartment: WATER1 Unconditional Global

$$d\text{WATER1}/dt = \text{RAIN} - \text{DR1} - \text{Evapo} - \text{UP1}$$
 Initial Value = 22
 compartment: WATER10 Unconditional Universal

$$d\text{WATER10}/dt = +\text{DR9} - \text{DR10} - \text{UP10}$$
 Initial Value = 22
 compartment: WATER11 Unconditional Global

$$d\text{WATER11}/dt = +\text{DR10} - \text{DR11} - \text{UP11}$$
 Initial Value = 22
 compartment: WATER12 Unconditional Global

$$d\text{WATER12}/dt = +\text{DR11} - \text{DR12} - \text{UP12}$$
 Initial Value = 22
 compartment: WATER13 Unconditional Global

$$d\text{WATER13}/dt = +\text{DR12} - \text{DR13} - \text{UP13}$$
 Initial Value = 22
 compartment: WATER14 Unconditional Global

$$d\text{WATER14}/dt = +\text{DR13} - \text{DR14} - \text{UP14}$$

Initial Value = 22
 compartment: WATER15 Unconditional Global
 $dWATER15/dt = +DR14-DR15-UP15$
 Initial Value = 22
 compartment: WATER2 Unconditional Global
 $dWATER2/dt = +DR1-DR2-UP2$
 Initial Value = 22
 compartment: WATER3 Unconditional Global
 $dWATER3/dt = +DR2-DR3-UP3$
 Initial Value = 22
 compartment: WATER4 Unconditional Global
 $dWATER4/dt = +DR3-DR4-UP4$
 Initial Value = 22
 compartment: WATER5 Unconditional Global
 $dWATER5/dt = +DR4-DR5-UP5$
 Initial Value = 22
 compartment: WATER6 Unconditional Global
 $dWATER6/dt = +DR5-DR6-UP6$
 Initial Value = 22
 compartment: WATER7 Unconditional Global
 $dWATER7/dt = +DR6-DR7-UP7$
 Initial Value = 22
 compartment: WATER8 Unconditional Global
 $dWATER8/dt = +DR7-DR8-UP8$
 Initial Value = 22
 compartment: WATER9 Unconditional Global
 $dWATER9/dt = -DR9+DR8-UP9$
 Initial Value = 22
 variable: WLG Conditional Universal
 WLG =
 (Upot*TE)/sdvp by default
 variable: WSTRESS Unconditional Universal
 $WSTRESS = \min((WLG/LLG),1)$
 variable: Z1 Unconditional Global
 $Z1 = 1-(\beta^{10})$
 variable: Z10 Unconditional Global
 $Z10 = (1-(\beta^{100}))$
 variable: Z11 Unconditional Global
 $Z11 = (1-(\beta^{110}))$
 variable: Z12 Unconditional Global
 $Z12 = (1-(\beta^{120}))$
 variable: Z13 Unconditional Global
 $Z13 = (1-(\beta^{130}))$
 variable: Z14 Unconditional Global
 $Z14 = (1-(\beta^{140}))$
 variable: Z15 Unconditional Global
 $Z15 = (1-(\beta^{150}))$
 variable: Z2 Unconditional Global
 $Z2 = (1-(\beta^{20}))$
 variable: Z3 Unconditional Global
 $Z3 = (1-(\beta^{30}))$


```

variable: Z4 Unconditional Global
Z4 = (1-(beta^40))
variable: Z5 Unconditional Global
Z5 = (1-(beta^50))
variable: Z6 Unconditional Global
Z6 = (1-(beta^60))
variable: Z7 Unconditional Global
Z7 = (1-(beta^70))
variable: Z8 Unconditional Global
Z8 = (1-(beta^80))
variable: Z9 Unconditional Global
Z9 = (1-(beta^90))
Temperaturemodule
variable: TSTRESS Conditional Universal
TSTRESS =
  (Tmean-Tbase)/(Tlowerthreshhold-Tbase) for Tmean<Tlowerthreshhold
  (Tmean-Tupperthreshhold)/(Thigh-Tupperthreshhold) for Tmean>Tupperthreshhold
  1 by default
Weathermodule
define value: THERMALTIME Unconditional Universal
THERMALTIME = 0.0001
independent event: THERMALTIMEevent Universal Active Reset
Period: 1
0
Actions:
Tmean=(Tmax+Tmin)/2;
THERMALTIME=0;
for (i=1; i<25; i=i+1) {
Ti=Tmean+0.5*abs(Tmax-Tmin)*cos(0.2618*(i-14));
THERMALTIME=THERMALTIME+(Ti-Tbase)/24
}
define value: Ti Unconditional Universal
Ti = 15
define value: Tmean Unconditional Universal
Tmean = 0
compartment: TT Unconditional Universal
dTT/dt = Thermaltime
Initial Value = 0.0001
lookup file: WEATHER C:\BAMGRO\Weather files\Weather 2007\UNISWA-33.txt
t Control
SRAD Controlled by: t Universal
  Start value interpolation
Tmax Controlled by: t Universal
  Start value interpolation
Tmin Controlled by: t Universal
  Start value interpolation
RAIN Controlled by: t Universal
  Linear interpolation
SDVP Controlled by: t Universal
  Linear interpolation

```