Samson Huni

Gas exchange, evapotranspiration efficiency, morphophysiology and productivity of cowpeas under water deficit

Cuvillier Verlag Göttingen
Internationaler wissenschaftlicher Fachverlag

Gas exchange, evapotranspiration efficiency, morphophysiology and productivity of cowpeas under water deficit

Dissertation

zur Erlangung des akademischen Grades *doctor rerum agriculturarum* (Dr. rer. agr.)

eingereicht an der Landwirtschaftlich-Gärtnerischen Fakultät der Humboldt-Universität zu Berlin

von Dipl.-Ing. agr. **Samson Huni**

geboren am 12.04.1968 in Makoni/Zimbabwe

Präsident der Humboldt-Universität zu Berlin:

Prof. Dr. Christoph Markschies

Dekan der Landwirtschaftlich-Gärtnerischen Fakultät:

Prof. Dr. Frank Ellmer

Gutachter:

1. Prof. Dr. Helmut Herzog
2. Prof. Dr. Eckhard George
3. Dr. Klaus-Peter Götz

Tag der mündlichen Prüfung: 23. Juli 2010

Bibliografische Information der Deutschen Nationalbibliothek
Die Deutsche Nationalbibliothek verzeichnet diese Publikation in der Deutschen Nationalbibliografie; detaillierte bibliografische Daten sind im Internet über http://dnb.d-nb.de abrufbar.
1. Aufl. - Göttingen : Cuvillier, 2010
Zugl.: Berlin, Humboldt-Universität., Diss., 2010

978-3-86955-599-7

Nonnenstieg 8, 37075 Göttingen
Telefon: 0551-54724-0
Telefax: 0551-54724-21
www.cuvillier.de

1. Auflage, 2010
Gedruckt auf säurefreiem Papier

978-3-86955-599-7

SUMMARY

The cowpea [*Vigna unguiculata* (L.) Walp.], a legume which originated in Africa, is now grown in the Tropics and many subtropical regions. Cowpea is of significance for food and feed and its yield is frequently severely affected by drought, resulting in its low average yield. Hence the influence of water deficit on gas exchange, growth, development and yield of cowpea was studied here, with the aim of contributing to our understanding of the response of cowpeas to water deficit and to the provision of efficient and viable information for breeding of drought resistant genotypes. To achieve this aim, several traits were examined, which included

- gas exchange [stomatal conductance (g_s), net photosynthetic rate P_N), transpiration rate (E) and intrinsic transpiration efficiency TE_i)], evapotranspiration efficiency (ETE), water use (WU) and yield/yield components,
- relationship among these traits and variability among the various genotypes.

From the results it was expected that it would be possible to find efficient plant types and characteristics to predict ETE and yield which could eventually be used in cowpea drought resistance breeding programmes.

For this purpose three pot experiments were conducted in the greenhouse under drip irrigation. The control (well-watered treatment) was irrigated continuously from the beginning to the end of the experiments, while the water-deficit treatment experienced a reduced irrigation resulting in a soil water potential of -350 to -450hPa at the onset of flowering for 14 to 21 days. Measurement and analyses of various traits were carried out before the induction of water-deficit stress, during and at the end of stress. All remaining plants were then fully irrigated up to the end of the experiments. In experiments 1 and 2 the plants were harvested at maturity to determine yield and yield components, and biomass and ETE.

Water-deficit stress impacted on all analysed traits and there were variations among genotypes in both treatments. Water deficit elicited the reduction of leaf relative water content and stomatal conductance. Consequently, P_N and E declined as well. However, E decreased more than P_N due to the influence of stress, generally leading to a higher TE_i of the water-deficit treatment. There were differences among experiments, probably due to interactions between the genotypes and the

environment. After stress, gas exchange recovered to similar levels of the control treatment. Biomass production, water use and evapotranspiration efficiency varied among genotypes within and between treatments. Compared with the control, water use and growth rate decreased clearly under stress. The role of P_N for biomass production became evident in the positive correlation between both parameters. TE_i had no distinct relationship to ETE.

Three traits, specifically leaf temperature (ΔT), leaf senescence (expressed as leaf shedding score, LSS) and cell membrane stability (CMS, calculated from electrolyte leakage values) distinguish themselves as valuable tools for drought resistance analysis. ΔT rose up to 3°C higher under stress than well-watered conditions. LSS increased under stress as well, whereby the genotypes which shed a relative high number of leaves under well-watered conditions also shed an even higher amount of leaves under stress. The sole genotype which retained all its leaves under stress, UCR 328, maintained all its leaves green, which was probably tremendously valuable for a quick recovery of different plant processes after stress. ΔT was consistently positively correlated with LSS, but negatively with CMS, particularly under stress. ΔT and LSS also displayed significant relationships with ETE, TE_i, grain yield and harvest index (HI). Owing to the fact that ΔT and LSS are simple, fast, cheap and non-invasively determined, they could be used in drought resistance breeding programmes as indirect selection traits for efficient plant types regarding transpiration, TE_i, ETE and yield.

The various genotypes yielded differently and the HI also varied under both treatments, a probable indication of differing genotypic yield potential. Water deficit at flowering reduced yield, but some genotypes had a higher HI. Generally, the genotypes with a high “yield potential” also manifested a higher yield under stress. TVu 12348 had the highest yield stability, but a low yield potential. UCR 328 and IFH 27-8 had a relatively high yield stability coupled with a high yield under stress.

ZUSAMMENFASSUNG

Die Kuh- oder Augenbohne [*Vigna unguiculata* (L.)Walp.] ist eine aus Afrika stammende Leguminose, die heute überall in den Tropen und in manchen subtropischen Regionen angebaut wird. Ihrer großen Bedeutung als Lebens- und Futtermittel stehen oft durch Wassermangel sehr geringe Erträge gegenüber. Deshalb soll in dieser Arbeit der Einfluss von Wassermangel auf Gaswechsel, Wachstum, Entwicklung und Ertrag der Kuhbohne untersucht werden mit dem Ziel, einen Beitrag zur Verbesserung des Verständnisses der Reaktion auf Wassermangel dieser Kulturpflanze zu leisten und für die Züchtung von dürreresistenten Sorten brauchbare Informationen zu erhalten. Um dies zu erreichen, wurden

- Gaswechsel [stomatäre Leitfähigkeit (g_s), Nettophotosyntheserate (P_N), Transpirationsrate (E) und intrinsische Transpirationseffizienz (TE_i)], ETE und Wassernutzung (WN), Ertrag/Ertrags-komponenten
- Variabilität der genannten Eigenschaften unter den Genotypen

untersucht. Aus den Ergebnissen sollte gefolgert werden, welche Pflanzentypen effizient sind und welche Eigenschaften für die Vorhersage der ETE und des Ertrags geeignet sind, die eventuell in der Züchtung auf Trockenresistenz verwendet werden können.

Dazu wurden drei Gefäßversuche mit je neun Kuhbohnen-Genotypen im Gewächshaus unter Tröpfchenbewässerung durchgeführt. Die Kontrollgruppe wurde durchgehend bewässert, während die Versuchsgruppe am Anfang der Blüte einem Wassermangel von 14 bis 21 Tagen bei einem Bodenwasserpotential von -350 bis -450 hPa, je nach Versuch, ausgesetzt wurde. Messungen und Analysen verschiedener Merkmale wurden kurz vor der Wassermangelbehandlung, während und am Ende des Stresses vorgenommen. Danach wurden alle Pflanzen bis zum Ende der Versuche voll bewässert und in den ersten zwei Versuchen nach der Vollreife geerntet, um sowohl Kornertrag und Ertragskomponenten als auch Trockensubstanz der Pflanzen zu bestimmen.

Trockenstress beeinflusste alle untersuchten Eigenschaften und es gab in beiden Behandlungen Unterschiede zwischen den Genotypen. Wassermangel führte zur Verringerung des relativen Wassergehaltes der Blätter und der stomatären Leitfähigkeit. Dadurch fielen auch die P_N und E herab. E wurde jedoch mehr negativ beeinflusst als P_N. Deshalb war TE_i der trockenstress-

behandelten Pflanzen höher als die der Kontrollpflanzen. Es gab Unterschiede zwischen den Versuchen. Das ist auf Interaktionen zwischen Genotypen und der Umwelt zurückzuführen. Nach Beendigung des Stresses erholte sich der Gaswechsel. Trockenmasse- (TM) Produktion, Wassernutzung (WN) und Evapotranspirationseffizienz (ETE) waren unterschiedlich für die verschiedenen Genotypen innerhalb der und zwischen den beiden Behandlungen. Im Vergleich zur Kontrolle fielen WN, Wachstumsrate deutlich geringer aus. Die Rolle von P_N in der TM-Produktion wurde in der positiven Korrelation zwischen beiden Parametern deutlich. TE_i hatte keine deutliche Beziehung zu ETE.

Hervorzuheben sind drei weitere Eigenschaften, nämlich Blatttemperatur (ΔT), Blattabwurf (LSS) und Stabilität der Zellmembran (CMS, gemessen als Elektrolytausfluss). ΔT erhöhte sich um bis zu 3°C unter Stress. Ebenfalls erhöhte sich Blattabwurf, wobei die Genotypen, die relativ viele Blätter unter ausreichendem Wasserangebot verloren auch deutlich mehr Blätter unter Stress abwarfen. UCR 328 war der einzige Genotyp, der keine Blätter unter Wassermangelstress verloren hat, alle Blätter blieben grün und das war wahrscheinlich von enormer Bedeutung für eine rasche Erholung der Pflanzen nach Ende des Stresses. ΔT war stets positiv mit LSS, aber negativ mit CMS, vor allem unter Stress, korreliert. ΔT und LSS waren auch mit ETE, TE_i, Kornertrag, und Ernteindex (HI) korreliert. Dadurch, dass diese zwei Parameter einfach, schnell, preiswert und Pflanzen schonend bestimmt werden, könnten sie in der Züchtung als indirekte Selektionsparameter für effiziente Pflanzentypen hinsichtlich von Transpiration, TE_i, ETE und Ertrag unter Wassermangelstress eingesetzt werden.

Es gab unterschiedliche Kornerträge und Ernteindices bei den verschiedenen Genotypen unter beiden Bedingungen, wahrscheinlich ein Zeichen des genotypisch unterschiedlichen Ertragspotentials. Wassermangel zur Blüte reduzierte den Ertrag, aber bei manchen Genotypen erhöhte sich dagegen der Ernteindex. Allgemein war bei den Genotypen mit hohem „Ertragspotential“ auch höhere Erträge in der Stressbehandlung zu verzeichnen. TVu 12348 hatte die höchste Ertragsstabilität, aber ein geringes Ertragspotential, während UCR 328 und IFH 27-8 eine relativ hohe Ertragsstabilität gekoppelt mit hohem Ertrag unter Stress aufwiesen.

Dedication

I dedicate this thesis to my wife, Renate, for all her love, inspiration, support and enduring patience. Thanks for sharing my life. Also to my children, Nyasha and Valentine, for continually reminding me that raising children is a huge challenge, certainly not a part-time job, but always rewarded with the joy of discovering something new, and discovering and inventing oneself anew. And to my parents, who no longer had enough time in this world to wait and see this work come to fruition – their conviction that education is one of the most valuable possessions a person can have – inspired me to go this far.

ACKNOWLEDGEMENTS

PhD research is never a lonely process, where one labours alone and for oneself. During the course of my research work I have met and worked with many people who helped and supported me in various ways.

I am indebted to my supervisor Prof Dr H. Herzog for the invaluable guidance and advice, keen interest and constructive criticism throughout my PhD studies and for his assistance in the preparation of this thesis.

The enormous interest, enthusiasm, valuable suggestions and help from Dr K.-P. Götz and Prof Dr R. Hoffmann-Bahnsen are greatly appreciated. I extend my sincere gratitude to Prof Dr E. George for accepting, at short notice, to read and evaluate my thesis.

I am very grateful to Ms S. Moryson for the great time we had in the greenhouse and lab, and all the HUB staff at Berlin-Dahlem (ATW5) for being there at various stages and for their encouragement and the kind co-operation extended to me during my work. I also acknowledge the input of my colleagues Dr Y. Y. Emendack, Ms S. Busch and Ms C. Sanetra.

To Ms B. Haack and Ms N. Fiensch special thanks for your contribution to the easy, joyous and comfortable working conditions in the Department.

I wish to express my gratitude to everyone involved, not mentioning names for fear of omitting anyone who has supported or helped me.

I would also like to express my gratitude and respect to Bettina and Johanna Markmeyer, Ekkehard Körber, my brothers and sisters, and parents-in-law. For their endless support and patience, my diction is too poor to express into words the gratitude I feel and owe them.

Table of contents

List of Tables

List of Figures

ABBREVIATIONS

ALVPD	air-to-leaf vapour pressure deficit (Pa kPa^{-1})
CMS	cell membrane stability (%)
DAP	days after planting (days)
DM	dry mass/matter (g) (refers here to shoot biomass only)
DM_{int}	dry mass/matter (g) produced during the stress interval
DMRT	Duncan's Multiple Range Test
DSI	drought susceptibility index
E	transpiration rate (mmol m^{-2} s^{-1})
ETE	evapotranspiration efficiency (g DM L^{-1} H_2O)
Exp	experiment
g_s	stomatal conductance (mmol m^{-2} s^{-1})
HI	harvest index
hPa	hectoPascal
LA	leaf area (cm^2)
LA_{int}	leaf area (cm^2) produced during the stress interval
LAR	leaf area ratio (shoot) (cm^2 g^{-1})
LMR	leaf mass ratio (shoot)
NAR	net assimilation rate of the shoot (g m^{-2} day^{-1})
P_N	net photosynthetic rate (µmol m^{-2} s^{-1})
RGR	relative growth rate (g g^{-1} day^{-1})
rH	air relative humidity (%)
RWC	leaf relative water content (%)
SGM	single grain mass (g)
SII	water deficit stress intensity index
SLA	specific leaf area (cm^2 g^{-1})
SMLR	stem mass to stem length ratio (g cm^{-1})
SMR	stem mass ratio
SSI	water deficit stress susceptibility index
StL	main stem length (cm)
StL_{int}	main stem length (cm) produced during the stress interval
SWC	soil water content (vol. %)
SWP	soil water potential (hPa)
ΔT	temperature differential (°C),
TDR	time domain reflectometer
TE_i	intrinsic transpiration efficiency (µmol CO_2 $mmol^{-1}$ H_2O)
wd	water deficit
WU	water use (L $plant^{-1}$)
WUE	water-use efficiency (g DM L^{-1} H_2O)
ww	well watered

1. INTRODUCTION

As cities and industry expand they are increasingly becoming serious competitors to agriculture for fresh water resources. In a world where about 70% of fresh water worldwide are committed to agriculture (UNEP, 2007; Barker *et al*., 1999), drought stress still remains one of the main constraints to crop productivity. Not only in water-limited environments, but also in other areas with more and better-distributed precipitation, crop yields can be depressed by up to 70% under good management without irrigation (Boyer, 1982). CO_2 assimilation thereby becomes increasingly limited through the effects of water deficit. These limitations can be caused by decreasing water content of the soil or by an atmospheric evaporative demand higher than the transpiration rate. With the global increase in population, climate change and decrease of arable land as a result of unsustainable agricultural procedures technological answers for efficient and sustainable crop water use have to be found and one way is to enhance the evapotranspiration and water-use efficiencies of crops (Andersen *et al*., 1999).

1.1. Aims and Objectives

Three experiments under continuous full irrigation or well-watered (ww) and water deficit (wd) conditions at the end of the vegetative stage and during the generative stage (flowering) were carried out between September 2003 and July 2005 with cowpeas [*Vigna unguiculata* (L.) Walpers], whose main objectives, under ww and wd conditions, were to:

- examine cowpea genotypic variation for gas exchange [stomatal conductance (g_s), net photosynthetic (P_N) and transpiration (E) rates] and to scrutinise the magnitude of genotypic responses under wd conditions
- determine and examine evapotranspiration efficiency and assess responses under wd conditions,
- establish the relationship between intrinsic transpiration efficiency and evapotranspiration efficiency
- examine yield and yield component variation among genotypes and to scrutinise the extent of genotypic yield responses under wd stress,
- assess expression of drought-tolerant traits among genotypes and their involvement in yield formation under wd stress conditions

- find out further traits like leaf temperature, leaf abscission and cell membrane stability, which are possibly related to intrinsic transpiration efficiency, evapotranspiration efficiency and yield, and finally
- identify
  - efficient plant types for water use or transpiration and stable relatively high yield
  - suitable surrogate traits for evapotranspiration efficiency and yield for use in breeding programmes.

2. LITERATURE REVIEW

2.1. Drought: Definition, importance/perspective

Drought is a complex phenomenon and a good definition of drought in the agricultural sense should include several aspects, some of which are precipitation, soil water content, evapotranspiration (actual and potential), and stage of development and types of crops. Drought is a protracted period with a lack of or insufficient precipitation accompanied by inadequate moisture in the soil and/or atmosphere, resulting in below average crop production being possible (NOAA, 2006). This lack of rainfall, which is highly heterogeneous over years and locations, is a primary abiotic stress causing not only yield loss but yield instability as well and can frequently be accompanied and compounded by other stresses like high temperature (leading to evapotranspiration rates that are higher than the rate of water uptake by the roots), salinity, and lack of nutrient availability. Soil variation in the field can be more pronounced when soil moisture is inadequate.

In the wake of climate change drought, together with the occurrence of high temperature, is predicted to be more prevalent and more severe in many parts of the world, e.g. in Southern Africa (IPCC, 2007) and water deficits are most likely in normally less susceptible regions with temperate climate e. g. Northeast and Central Germany (Schindler *et al.*, 2007). It is also predicted that global temperature will increase by about 1,5 to 6°C (IPCC, 2007) and global evapotranspiration by 5 to 10% (OTA, 1993) in the next 100 years. Both factors are bound to compound the already complicated problem of drought. Hence, given these climate change scenarios, it is worthwhile to study yield constraints under less favourable production conditions, especially under drought as the main abiotic stress. In a recent report regarding food security, The Royal Society (2009) came to a similar conclusion, where it made a call for focussed research and funding in order to enhance food production, particularly critical under an altered, less conducive climate, increasingly degraded soils and dwindling irrigation water availability.

2.2. Gas exchange, evapotranspiration efficiency, biomass accumulation and partitioning

Gas exchange has been reported to be affected by the availability of water in the soil and by the evaporative demand of the air. The transpiration and net photosynthetic (CO_2 assimilation) rates under water replete conditions is usually high and when the extractable

water in the soil is too low or the evaporative demand becomes too high, then this leads to stomatal closure (Bunting and Kassam, 1988; Sutcliffe, 1968). This closing of the stomata reduces to a larger extent transpiration but also photosynthesis. Stomatal conductance for water and CO_2 are affected directly before net photosynthetic and transpiration rates are negatively affected. As water and CO_2 use the same pores (stomata) to diffuse into and out of leaves, respectively, it is axiomatic that water has to be utilised in CO_2 assimilation, biomass accumulation and growth. It is this inevitable coupling of gas exchange which leads to the fact that water use and biomass production of cultivated plants are closely linked to each other (Ehlers, 1997).

Since the publication of the classic paper of Cowan and Farquhar (1977) on the basis of optimal function of stomata and enhancement of leaf gas exchange efficiency under diverse environmental conditions a lot of research has been carried out on different aspects of gas exchange and intrinsic or instantaneous transpiration efficiency (TE_i). In the literature TE_i has been termed, for example, simply transpiration efficiency or leaf level transpiration efficiency or even water-use efficiency. Condon and Hall (1997) point out that it should be possible to exploit genotypic variation for TE_i to ameliorate adaptation to specific environments and Franks and Farquhar (2007) emphasise that those genotypes with fast and appropriate response to environmental factors which impact on stomatal conductance (g_s), CO_2 assimilation and transpiration rates should have a higher TE_i. Since stomatal guard cells perceive and act on various signals in the aerial and soil environment so as to optimise the size of the stomatal opening thereby optimising CO_2 gain and H_2O dissipation (Jones, 1992; Cowan, 1982; Farquhar and Sharkey, 1982), stomata are importance in influencing ETE and WUE. At TE_i and WUE can be improved probably by not only decreasing stomatal aperture but also increasing CO_2 assimilation capacity (Bacon, 2004). However, at crop level there is a "decoupling effect" from the role of individual stomata like crop temperature dynamics and canopy boundary layer conductance which can be influenced by for example, leaf movements typical in some pulses like cowpeas, canopy structure, and so on. All the same, it has been suggested that TE_i based on g_s, that is the ratio A/g_s, should be a better and direct measure of the fundamental photosynthetic process since there is a process of normalisation (Medrano *et al.*, 2002; Farquhar *et al*., 1989).

Farquhar and co-workers and other researchers (e.g. Hall, 1995; Hubrick and Farquhar, 1989; Condon *et al*., 1987; Hubrick *et al*., 1986) have demonstrated that the heavier natural isotope

of CO_2 ($^{13}CO_2$) as opposed to the lighter one ($^{12}CO_2$) is discriminated against so that $^{13}CO_2$ is diluted in plant tissue (assimilates) compared to the natural atmosphere, but the level of this discrimination ($\delta^{13}CO_2$) depends on the crop species and genotype, and $\delta^{13}CO_2$ is related to ETE and WUE – a low $\delta^{13}CO_2$ being generally indicative of a high ETE and WUE. This relationship remains valid whether for TE_i or ETE (Evans *et al*., 1986; Farquhar and Richards, 1984). However, low $\delta^{13}CO_2$ alone does not necessarily lead to high ETE, especially if the high ETE is as a result of low stomatal conductance (g_s) under water replete conditions. At present new methods with oxygen isotopes (H_2O^{18} and H_2O^{16}) are being used to provide supplementary information on whether high ETE genotypes identified through low $\delta^{13}CO_2$ can also have a high productivity (high WUE) under well-watered and water deficit conditions (Barbour *et al*., 2000). Nevertheless, the $\delta^{13}CO_2$ method does not allow for determination of carbon losses through respiration nor for evaporation from the soil. Besides, all these isotope-based methods are expensive especially when applied in large breeding programmes in developing countries. The situation gets complicated by the fact that high ETE generally has a productivity cost (Jones, 2004). The ETE and WUE of plants are influenced by, among other things, water availability, species, genotype, nutrition and leaf-to-air vapour pressure deficit (VPD) and because VPD depends on air temperature (Eamus *et al*., 2008; Lambers *et al*., 1998), ETE and WUE ultimately are subject to the effect of temperature during the whole ontogeny of the plant or crop.

Growth, biomass partitioning and yield are affected negatively partly by lack of water in the soil as a result of of low stomatal conductance and photosynthesis. However, there are some other processes in the plant that are more sensitive to water deficit, namely leaf cell division and growth and protein synthesis (Bradford and Hsiao, 1982). Normally this leads to thicker but smaller leaves and roots are relatively less negatively affected by low soil water potential than the shoot. Insight into effects of water deficit on the whole plant and genotypic reactions can be furnished by analysis of growth rate, whereby the relative growth rate (RGR), net assimilation rate (NAR) and allocation of dry matter (DM) to different organs (DM partitioning) (Lambers *et al*., 1989; Gifford and Evans, 1981) are useful and reliable traits. However, RGR is considered by some as being not particularly appropriate to discern the relation between physiology and growth (Lambers *et al*., 1998). Instead, carbon dioxide assimilation, leaf area, specific leaf area and leaf mass ratio, respiration and DM allocation are suggested as more meaningful parameters. The formation of agronomic yield is then influenced by environmental conditions (water nutrient and availability, temperature, light,

VPD, etc) and genotype, since adaptation to environment and DM allocation to seeds (expressed as harvest index – ratio of seed DM to shoot DM) are affected by these two factors. The search for reliable morphological and physiological traits is still on-going (Richards, 2006; Araus *et al*., 2002).

2.3. Cowpeas

2.3.1 Ecophysiology, production and importance, constraints and drought research

Cowpea [*Vigna unguiculata* (L.) Walpers] is primarily autogamous (Purseglove, 1968; Summerfield *et al.*, 1983; Singh, 2005) and has its origin in Africa, with latest scientific information (Padulosi *et al.*, 1997) pointing towards Southern Africa as the origin of the cultivated cowpea and West Africa as the primary and the Indian subcontinent the secondary centre of diversity of cultivated cowpeas. Cowpea has various growth habits; from trailing, indeterminate and bushy types to non-trailing, erect and determinate types and can have deep roots. This species, of which many genotypes (especially the indeterminate medium to long duration types) are sensitive to effects of temperature and photoperiod (Ehlers and Hall, 1996; Wien and Summerfield, 1980; Wienk, 1963), is adapted to warm climates and needs warm soils to establish (Craufurd and Wheeler, 1999; Wien and Summerfield, 1984) and may take about 40 to 150 days to flower (de Moody, 1985).

Today, cowpea is cultivated in Africa, Asia, Australia, the Americas and southern Europe (Timko and Singh, 2008). This leguminous plant plays an important economic and agronomic role in different cropping systems because it is capable of fixing atmospheric nitrogen, a function anticipated to grow as sustainable agriculture develops (Serraj *et al*., 1999). Green leaves and pods of cowpea are used as fresh vegetables or dried to be eaten later in the dry season. The dry beans are prepared in different ways for human consumption and the haulms are used as quality fodder. Cowpeas are also utilised as cover crops and as green manure. The dry beans of cowpeas are rich in high quality protein (a good compliment for the protein-scant diet of the poor providing about 50% of plant protein in sub-Saharan Africa) and digestible carbohydrates, having an energy content almost equivalent to that of cereal grains (AATF, 2007). Dry beans have on average 20 – 27% protein, 0,4 – 3,3% fat and 56 – 66% carbohydrate (Table 1) (Singh, 1999; Fashakin and Fasanya, 1988). Cowpeas are regarded to be the principal grain legume in Africa's tropical dry savannas. Here, production is carried

out on over 12,5 million hectares, with almost 200 million people consuming cowpeas and most of the production is subsistence or for sale at local markets, (AATF, 2007).

	Seeds (%)	**Hay** (%)	**Leaves** (%)
Carbohydrate	55 – 65		8 – 9
Protein	20 – 28		5
Water	7 – 12	18	85
Crude fibre	4 – 7	10	2
Ash	3 – 4	23 – 24	2 – 4
Fat	0,5 – 3	11	0,3
Phosphorus	0,146	2,6	0,063
Calcium	0,1		0,3
Iron	0,005		0,005

Table 1: Chemical composition of seeds, hay and leaves of cowpea (after Chinma *et al.*, 2008; Henshaw, 2008; Singh, 1999; Fashakin and Fasanya, 1988; Khan *et al.*, 1979; Watt and Merrill, 1975**)**

Cowpeas are usually produced in hot and semi-arid regions under rain-fed conditions, where rainfall is unevenly distributed in the season and over the years. Diseases, pests and drought represent the main yield limitation for cowpea, particularly in Africa, with losses due to these three constraints often amounting to as much as 90% (AATF, 2007). Almost 70% of the production occurs in Africa, where the yield is very low. The unstable and poor yields of cowpea, however, can be ascribed mainly to the inconsistent and scant precipitation which can exacerbate the occurrence of pests and diseases (Watanabe *et al*., 1997). Nonetheless, research plots and production in North Africa, the Balkans and the USA have shown that yields from 4 tonnes (Ortiz, 1998) up to 7 tonnes (Sanden, 1993) per hectare are possible with cowpea.

Magnitude and quality of yield of crops decline due to drought and indirect drought effects (for example, disease and pest infestation (Agele *et al*., 2006)) at various growth stages. However, there are still differing opinions on the effects of water deficiency on yield at the vegetative stage up to visible flower bud growth, but a general agreement on the negative effects during the reproductive phase (especially at flowering and podding filling) already exists (Turk *et al*., 1980; Turk and Hall, 1980a; Hiler *et al*., 1972) especially for determinate genotypes. Differences in results might also be caused by differences in determining the level of drought stress which is complicated by the fact that cowpeas display an isohydric behaviour (opposed to anisohydric plants like sunflower and sorghum) and control stomatal conductance (g_s) so as to maintain daytime leaf and/or shoot water status almost constant, irrespective of soil water status (Tardieu, 1996; Bates and Hall, 1981). Jones (2007) and

Tardieu (1996) points out that drought stress in isohydric plants cannot be defined well by leaf or plant water status – especially leaf water potential, except when the stress is very severe. With changes in evaporative demand or soil water content isohydric plants tend to minimise changes in leaf or shoot water status (Jones, 2004; 1983). Besides, there are two types of drought tolerant genotypes in cowpea (Mai-Kodomi *et al*., 1999a; 1999b; Singh *et al*., 1997): type 1 terminate growth but retain most of their leaves for a long time and thus conserve soil water, whereas type 2 remobilise nutrients from lower leaves leading to a relatively fast senescence of lower leaves but the tips remain alive for a longer time than those of type 1.

The knowledge of physiology of gas exchange is now being used to produce drought tolerant genotypes in cereals. The first two drought tolerant cultivars of wheat were bred based on $\delta^{13}C$, TE_i, ETE and WUE, and released in the last 10 years (Munns and Richards, 2007; Richards, 2006; Condon *et al*., 2004) in Australia. In grain legumes, however, such breeding success in this area has remained illusive. Compared with other legumes cowpea has a better adaptation to drought, although drought remains one of the major constraints to high productivity of this legume in all the major cowpea production regions of the world and drought is set to get worse subsequent to climate change. Investing, among other things, in developing drought tolerant varieties of cowpea insures against erratic rainfall and stabilises agricultural output, boosts crop productivity and can allow farmers to diversify and can immensely contribute to food security in Africa. Besides, the inclusion of legumes like cowpeas in crop rotation is increasingly being advocated in order to improve the sustainability of cereal crop production, thus reducing environmental pollution with nitrogen fertilisers and checking the increase of soil pathogens (Loomis and Connor, 1992).

In breeding, utilisation of physiological traits in screening programmes is still limited. One of the reasons is partly due to physiological traits being indirectly related to yield (Araus, 1996; Richards, 1996). Sometimes there is scant knowledge of the crop ecophysiology, particularly if breeding for yield is conducted under water-limited conditions (Araus *et al*., 2001). Besides transpiration and net photosynthetic rates, stomatal (and mesophyll) conductance is a significant gas exchange trait which has been shown to be a reliable trait linked to grow and yield (Jiang *et al*., 2006; Medrano *et al*., 2002).

3. MATERIALS AND METHODS

3.1. Plant material

Nine, non-nodulated cowpea genotypes from different countries in Africa, Asia and the Americas were used. The genotypes were chosen to stand for these main cowpea production regions. Rhizobia and their activity in symbiosis are known to be highly sensitive to drought stress (Kirda *et al*., 1989; Zablotowicz *et al*., 1981; Sprent, 1972), although Streeter (2003) argues against this general assumption. Thus, a further complication in the reaction of the cowpea plants to water deficit stress was avoided by precluding the use of rhizobia in these experiments. Further criteria for the choice of the genotypes were that they had to be upright, non-creeping, non-bushy and no late maturing genotypes. Although bushy and creeping genotypes are frequently encountered in small-scale farmers' fields, they are difficult and cumbersome to work with in the confines of a greenhouse, are sometimes late maturing and sensitive to photoperiod (Wien and Summerfield, 1980; Wienk, 1963). Therefore early to medium genotypes were chosen in preference to long season ones. Some known released cultivars, in this case IT 18 and Vita 7, were also included. Table 1 shows the genotypes used for these experiments and their origin. Most of the genotypes are from Nigeria because the International Institute of Tropical Agriculture (IITA) is situated there, which has done tremendous work on cowpea breeding, germplasm collection and storage, and research. The other genotypes are from Seed Company of Zimbabwe (SeedCo) and USA URS Genebank.

Designation	Genotype	Origin	Seed Source
ExU	Ex Ukwala	Kenya	IITA
U328	UCR 328	Nigeria	IITA
U1340	UCR 1340	India	URS
IT18	IT 18	Zimbabwe	SeedCo
U386	UCR 386	Nigeria	IITA
Lag	Lagreen	USA	URS
Vit	Vita 7	Nigeria	IITA
TVu	TVu 12348	Nigeria	IITA
IFH	IFH 27-8	Nigeria	IITA

Table 2: The cowpea genotypes used in these studies, their designations in these experiments, countries of origin and the seed source.

3.2. Pots, growth substrate and planting

PVC pots with a length of 0,50 and diameter of 0,16 m, giving a volume of about 10 L, were used in all the three experiments. The end plate at the bottom of each pot had six holes to allow drainage if there was excess water in the pot. Each pot was filled with 14 kg sand and the sand was divided into two layers: pot zone 1 was the bottom zone containing 11 kg of sand and more mineral nutrients as opposed to zone 2 at the top of the pot with only 3 kg of sand and less nutrients. Pot zone 2 got less nutrients (70% less) so as to avoid negative effects from the nutrients on the young and few roots of the seedlings, especially after planting. About 2 cm of fine quartz gravel were applied at the top of the pot to significantly reduce evaporation from the substrate surface.

Sieve size (mm)	Mass (%)	Type of particle
2 – 6	4,8	Fine gravel
0,20 – 0,30	76,9	Coarse to medium sand
<0,10 – 0,15	18,3	Fine sand

Table 3: The composition of the sand (substrate) used in all experiments

The growth substrate (sand) used throughout was cleaned river sand mixed with nutrient salts and some organic matter. The use of sand as a growth substrate was preferred because sand dries down fast and uniformly, and can be remoistened very fast, uniformly and the water is immediately available to plants. The sand in every pot was slightly compacted to give the required bulk density of 1,5 to 1,6 g cm^{-3} to guarantee good plant growth and reliable determination of substrate water potential using tensiometers. The composition of the sand can be seen in Table 3 above. The nutrient mixture used to mix with sand consisted of the substances indicated in Table 4, modified according to Hoffmann-Bahnsen (1996).

The biggest and best seeds of the genotypes were selected and then pre-germinated at about 25°C for 72 hours on wet filter paper in a germination tray placed on a bench in the laboratory. Six pre-germinated seeds were then planted per pot. Two weeks later thinning was undertaken leaving only the best two seedlings in each pot. Staggering of the planting of the various genotypes was carried out so as to synchronise flowering of all genotypes. The growth and development, and other information of these genotypes had been obtained in two preliminary experiments.

Nutrient	Amount in zone 1 (mg)	Amount in zone 2 (mg)
N	190	1600
P_2O_5	160	1350
K_2O	190	1700
Mg	130	1100
S	125	1000
Cu	6	60
B	3	25
Fe	18	150
Zn	8	80
Mn	2	13
Mo	0,3	3
Co	0,4	2

Table 4: Nutrient amounts applied to each pot in pot zone 1 and 2, where pot zone 1 were the top 3.0 kg substrate and pot zone 2 the 11.0 kg below zone 1.

3.3. Conditions of culture

3.3.1. Irrigation system

Throughout all these studies an automatic drip irrigation system was used, programmed to irrigate four to eight times as required during the whole day (04:00h – 22:00h), and controlled by tensiometers (Irrometer, Irrometer Company Riverside, California/USA) placed 25 cm in a reference pot for each irrigation station (Fig. 1). All four to six pots of one station contained plants of a particular genotype and treatment. However, irrigation was manual (2 times each day) in the first two weeks after planting since the plants did not require much water at the seedling stage. In order to guarantee sufficient nutrient supply for all plants at all times a supplementary 100 mL of a 0,3% Wuxal® nutrient solution (AGLUKON Spezialdünger GmbH & Co. KG, Düsseldorf, Germany) (containing all nutrients as shown in Table 3) was applied manually per pot on a biweekly basis from day 29 after planting.

Substrate water potential (SWP) was monitored on a daily basis using tensiometers and the substrate water content (SWC) was measured every other day (at most three times a week) using time domain reflectometer (TDR) (TDR Soil Moisture Meter FOM/m/92, Easy Test Ltd, Lublin/Poland) probes permanently placed horizontally in the pots at a depth of about 20cm. Results of preliminary experiments showed that substrate field capacity was at -70 to -80 hPa (tensiometer) corresponding to about 10 volumetric % (TDR).

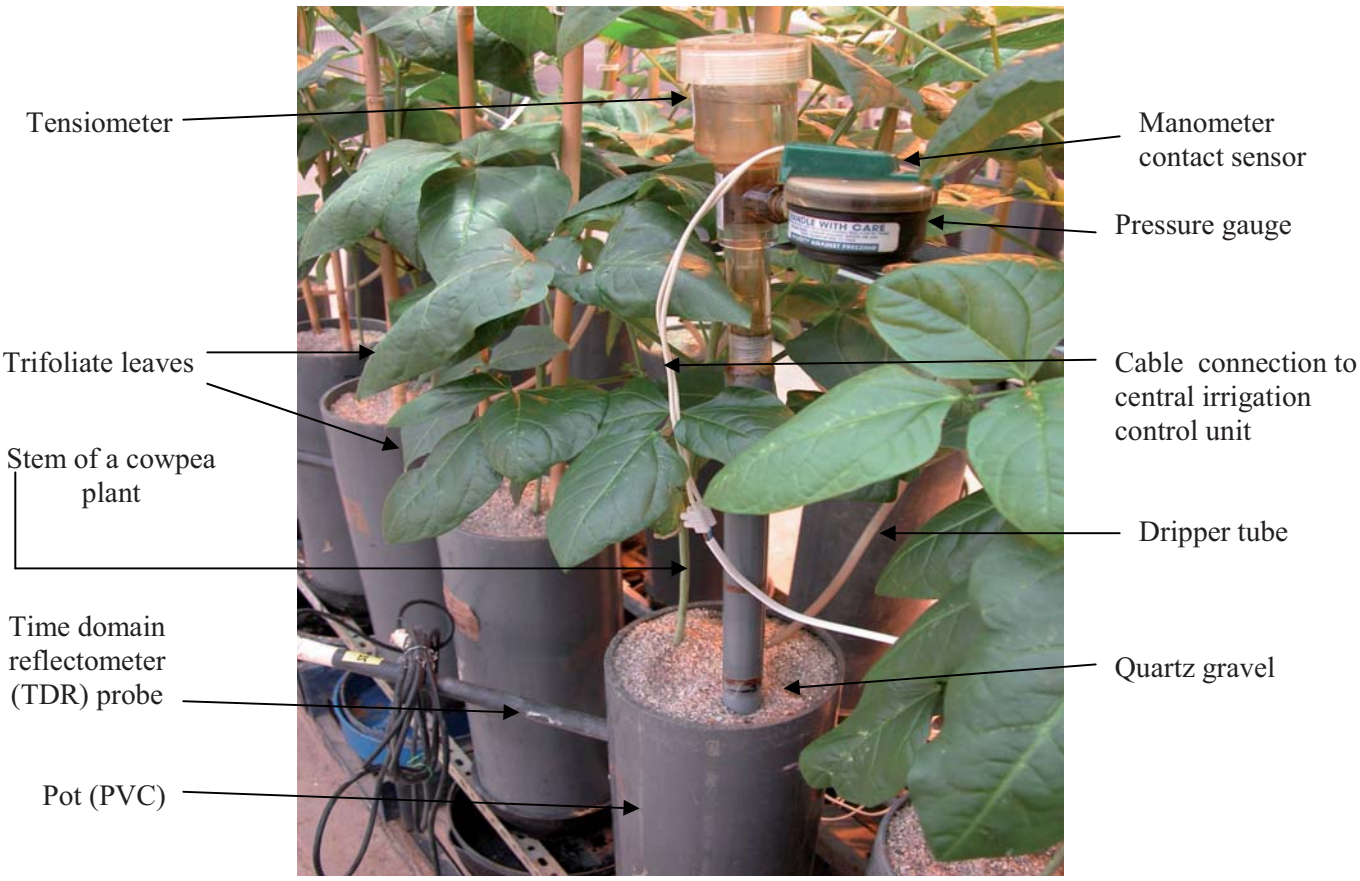

Fig. 1: General experimental set-up typical for all experiments conducted in these studies

Well-watered treatments, on the one hand, were not allowed to go below -80 hPa or 7,5% SWC and on the other hand water deficit treatments in the maximum stress duration were maintained at -300 to -400 hPa (or 4 – 5% SWC) for experiments 1 and 2, and for experiment 3 at -400 to -500 hPa (or 3 – 4% SWC). Sometimes it was necessary to apply water manually to adjust the SWP or SWC to the required levels.

3.3.2. Light, Temperature and Relative Humidity

Experiments 1 and 2 were carried out in winter from mid-September to mid-March of the following year. The photoperiod used in these two experiments was 13 hours light (Osram Powerstar HQI-TS 400 W/D) and 11 hours darkness. The photosynthetic photon flux density (PPFD) provided by these lamps was about 200 – 300 µmol m^{-2} s^{-1} at the top of the canopy.

The temperature in the greenhouse was kept at 25 to 29°C during the light period (day) and 15 to 18°C during the dark period (night). In experiment 3 the photoperiod was higher than in the

first two experiments because this experiment was conducted from mid-April to the beginning of August 2005 during which temperatures were also higher (minimum of 17 – 20°C and maximum of 27 – 32°C) and PPFD was also higher (about 400 – 500 µmol m^{-2} s^{-1}). In all the experiments a relative humidity of 35 to 45% during the light period and 75 to 85% during the dark period was maintained.

3.4. Gas exchange measurements

Gas exchange (water vapour and carbon dioxide) was measured on the third or fourth leaf from the main stem apex (only main stem leaves were taken into consideration for gas exchange measurements) using a steady state porometer (CQP 130i, Walz Meß- und Regeltechnik, Germany), which sucked greenhouse air through a filter into a 100L buffer tank to reduce the effect of short-term flactuation of CO_2 and water in ambient air. The air was then pumped to the leaf at a rate of 900 mL $minute^{-1}$. During the gas exchange measurements light in the cuvette was maintained at a PPFD of 800 – 850 µmol m^{-2} s^{-1} with the assistance of an extra external light source. The measurements were carried out on 5 cm^2 of one of the lateral leaflets of the third or fourth fully developed leaf from the apex, but not on the middle leaflet. Thus, standard leaves obtained on which gas exchange and other traits were measured. A sensor at the abaxial side of the leaf in the cuvette determined leaf and cuvette temperature in order to keep the cuvette temperature close to the ambient temperature. Besides, air relative humidity (RH) in the cuvette was also monitored. Water and CO_2 were determined by the infrared gas analyser that is an integral component part of the porometer and the actual measurements were conducted when steady state conditions prevailed. These measurements were performed on two consecutive days between 08:30h and 15:30h. From these measurements stomatal conductance (g_s), net photosynthetic rate (P_N) and transpiration rate (E) were derived after calculations according to von Caemmerer and Farquhar (1981).

3.5. Leaf relative water content and leaf relative electrolyte leakage

Leaf relative water content (RWC) was determined according to the standard method (Barrs and Weatherley, 1962). In experiment 2 and 3 RWC was determined on the leaves where gas exchange had been measured. Avoiding large leaf veins, leaf discs (14 mm diameter) were quickly punched out of those leaves using a sharp cork borer between 11:30h and 13:30h, placed in a picnic cooler (about 15°C) and then weighed in the laboratory (fresh mass, FM)

within ten minutes of punching. Subsequently, the leaf discs were floated on 5 mL of deionised water in closed vials and left for four hours under normal room light and temperature (21 – 23°C). At the end of the four hours the leaf discs were removed from the vials, quickly blotted dry, and weighed again to determine the turgid mass (TM). After that the discs were oven dried at 80°C for 24 hours, at the end of which the cooled discs were weighed to establish the dry mass (DM). The formular applied to determine the RWC was as follows: **(FM – DM)/(TM – DM)*100**.

In experiment 2 and 3 cell membrane stability (CMS) was determined according to the method of Tripathy *et al*. (2000), whereby five leaf discs (as for RWC) from one plant were washed and then incubated in a sealed test tube for 24 hours in 20 mL of deionised distilled water in a dark cupboard. At the end of incubation electrical conductivity (EC_1) was measured using an electrical conductivity meter (Microprocessor Conductivity Meter LF539, WTW/Germany). Then the glass test tubes containing the leaf discs were autoclaved at 140°C for 20 minutes followed by incubation for 24 hours in a dark cupboard at room temperature. A second electrical conductivity measurement (EC_2) was carried out. CMS of the wd treatment was calculated according to the formular: **CMS (%) = [1-(EC_{1wd}/EC_{2wd})]/[1-(EC_{1ww}/EC_{2ww})]*100**, where subscripts wd and ww stand for water deficit and well-watered treatment, respectively. A second method to evaluate electrolyte leakage was applied, whereby simple relative electrolyte leakage was determined separately for the ww and wd treatments as follows: **(EC_1/EC_2)*100**.

3.6. Biomass, leaf area, leaf temperature and stem length

Plant shoots were harvested at three sampling dates: before stress (bs), stress end or maximum stress (se) and at maturity. At the first two sampling dates the length of the main stem was measured, the number of nodes on the main stem counted and then the shoots were separated into leaves (petioles were left on the main stem/branches), main stem and branches. Leaf temperature was determined during the period of maximum wd stress using an infrared thermometer (*i*-tec 2003, *i*-tec Sensor-Messtechnik GmbH, Lüneburg/Germany) held at 90° 20 – 23 cm above one of the leaflets of the youngest fully developed leaf at the top of the main stem. The fresh mass of each of the three components was determined and the green leaf area immediately determined using a leaf area meter (Model 3100 Area Meter, Li-Cor BioSciences, Lincoln, Nebraska/USA). The area of all leaves which had a green area less than

50% of the leaf was not measured. Following this all shoot components were oven dried at 80°C for 72 hours and then weighed again to determine the dry mass, which was the basis for the appropriate calculation of some other parameters (Table 5) like evapotranspiration efficiency (ETE), specific leaf area (SLA), leaf area ratio (LAR), stem mass to stem length ratio (SMLR), stem mass ratio (SMR), leaf mass ratio (LMR), relative growth rate (RGR) and net assimilation rate (NAR).

Parameter	Formular	Units
SLA	Green leaf area/DM of these leaves	$cm^2\ g^{-1}$
LAR	Green leaf area of a plant/shoot biomass	$cm^2\ g^{-1}$
SMR	Stem DM/shoot biomass	
SMLR	Stem mass/stem length	$g\ cm^{-1}$
LMR	Leaf DM/shoot biomass	
RGR	(ΔShoot biomass /Δt) x (1/ Shoot biomass)	$g\ g^{-1}\ day^{-1}$
NAR	RGR/LAR	$g\ m^{-2}\ day^{-1}$
ETE	Shoot biomass/amount of water used	$g\ L^{-1}$
HI	Seed yield/shoot biomass at harvest	

Table 5: Some parameters calculated from leaf area, biomass and length, and the methods used to calculate them.

After the final seed yield was obtained in experiment 1 and 2, the water deficit stress susceptibility index (SSI) and the water deficit stress intensity index (SII) (Fischer and Maurer, 1978) were determined as follows:

$SII = 1 - (X_s/X_{ns})$, where X_s is mean experiment yield of all genotypes grown under drought stress and X_{ns} is mean experiment yield of all genotypes grown under non-stress conditions.

$SSI = [1 - (Y_s/Y_{ns})]/SII$, where Y_s is genotypic performance under stress conditions and Y_{ns} is genotypic performance under non-stress conditions

SII is a measure of the severity of water deficit stress based on yield, which permits values to be compared among experiments and environments.

4. RESULTS

Three experiments were carried out in a greenhouse from September 2003 to beginning of August 2005 with nine cowpea genotypes, whereby six were used in experiment 1 (Exp 1), the same six genotypes as in experiment 1 and three additional ones in experiment 2 (Exp 2), and seven genotypes (five as in Exp 1 and two of the additional ones in Exp 2) in experiment 3 (Exp 3). Exp 1 and 2 were similar in that the planting of the various genotypes was staggered (planted at different dates) so as to synchronise flowering time – according to data derived from two preliminary experiments. In Exp 3 all genotypes were planted on the same day and wd stress was induced on the same "physical" day regardless of the stage of development of each genotype, meaning that some of the genotypes were already close to flowering, while others were still in their vegetative phase, particularly Vita 7, UCR 386 and Lagreen. For brevity, mainly the results obtained in Exp 1 and Exp 2 are presented here, with special reference to Exp 3 only in particular sections.

Water deficit (wd) stress was successfully imposed in all three experiments. In experiments 1 and 2 wd stress was induced at the onset of flowering (visible flower buds), with wd stress in Exp 1 lasting 19 days (five days of drying down and 14 days at maximum stress of about -350 hPa) and in Exp 2 21 days (six days of drying down and 15 days of maximum stress of about -375 hPa). In Exp 3 wd stress remained for 18 days (six days of drying down and 12 days of maximum stress of about -400 hPa).

4.1. Growth conditions

4.1.1. Greenhouse temperature (T) and relative humidity (rH)

Although experiments 1 and 2 were conducted in the same greenhouse the conditions, in particular temperature and relative humidity (rH), differed somewhat. Regarding this aspect, experiment 1 having higher temperature and rH levels than experiment 2. However, the temperature trends were similar in both experiments (Fig. 2), in that there were approximately three different phases where temperature behaved similarly (i. e. high temperatures at the beginning, depressed temperatures in the middle of the experiments corresponding to winter and rising temperatures towards the end of the experiments). In experiment 3 both temperature and rH (Table 3) – but especially temperature – were higher than in the preceding experiments since it was carried out in spring and summer months (April to beginning of August 2005).

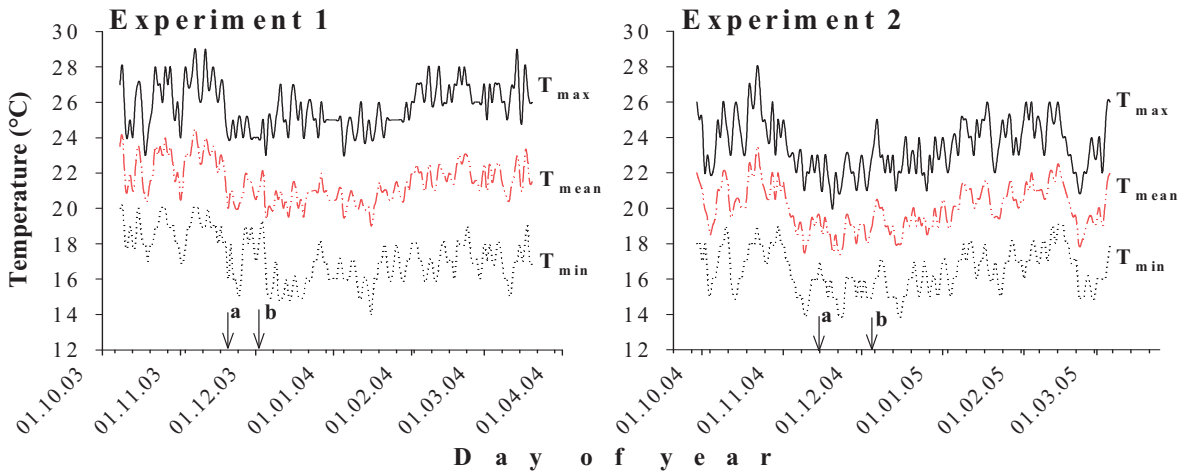

Fig. 2: Minimum, maximum and mean air temperature (°C) in the greenhouse starting three weeks after planting to maturity (experiment 1 and experiment 2). Arrows **a** and **b** denote stress begin/onset of flowering and end of stress, respectively.

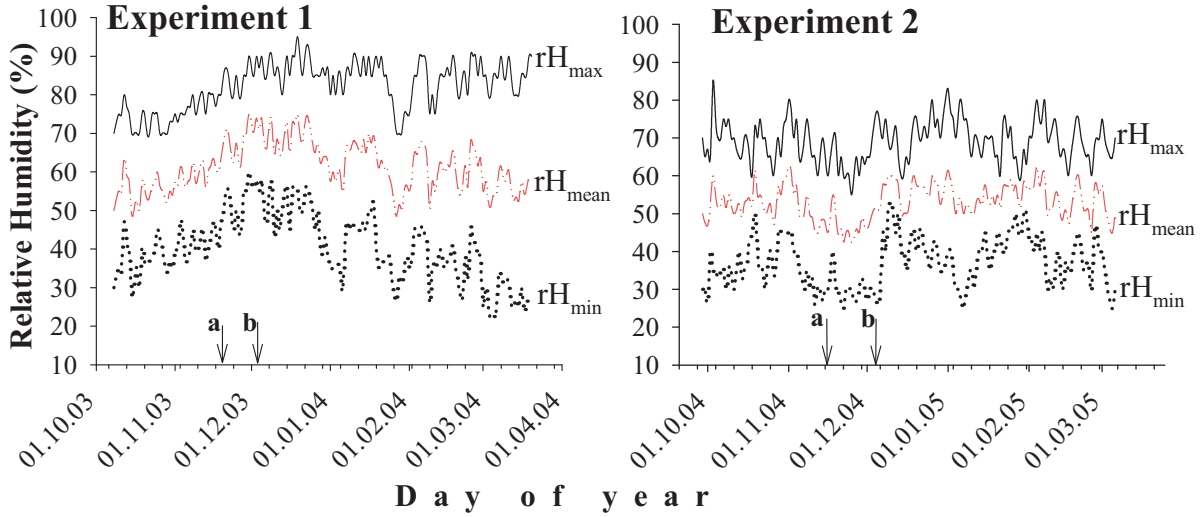

Fig. 3: The course of minimum (rH_{min}), maximum (rH_{max}) and mean (rH_{mean}) relative humidity (%) in the greenhouse starting about three weeks after planting to maturity in experiment 1 and experiment 2. Arrows **a** and **b** denote stress begin/onset of flowering and end of stress, respectively.

4.1.2. Soil water potential (SWP) and soil water content (SWC)

Before stress imposition, all pots had a similar soil water potential (SWP), typically ranging between -40 and -70 hPa (Fig. 4), in all three experiments. During stress, SWP fell to a minimum of about -370 hPa in the wd treatment (for about two weeks), while the ww treatment remained around -75 hPa. After relief from stress, the SWP of all treatments was maintained between -60 and -80 hPa for all pots.

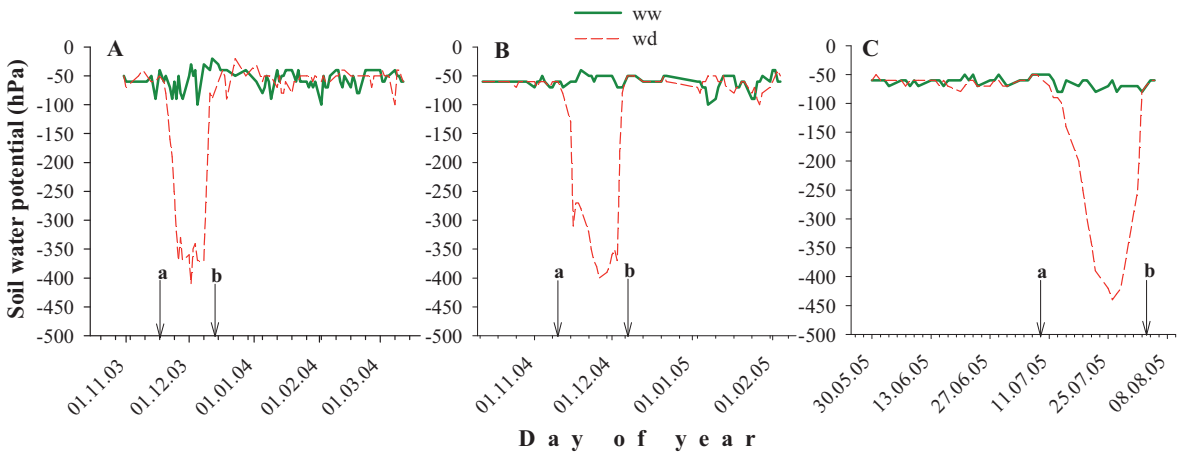

Fig. 4: Soil water potential, SWP (hPa) starting three weeks after planting to maturity in experiment 1 (**A**) and experiment 2 (**B**), or to the end of stress in experiment 3 (**C**) for the well-watered (ww) and water deficit (wd) treatments. Arrows **a** and **b** denote stress begin/onset of flowering and end of stress, respectively.

Before stress imposition, all pots had a similar soil water potential (SWP), typically ranging between -40 and -70 hPa (Fig. 4), in all three experiments. During stress, SWP fell to a minimum of about -370 hPa in the wd treatment (for about two weeks), while the ww treatment remained around -75 hPa. After relief from stress, the SWP of all treatments was maintained between -60 and -80 hPa for all pots.

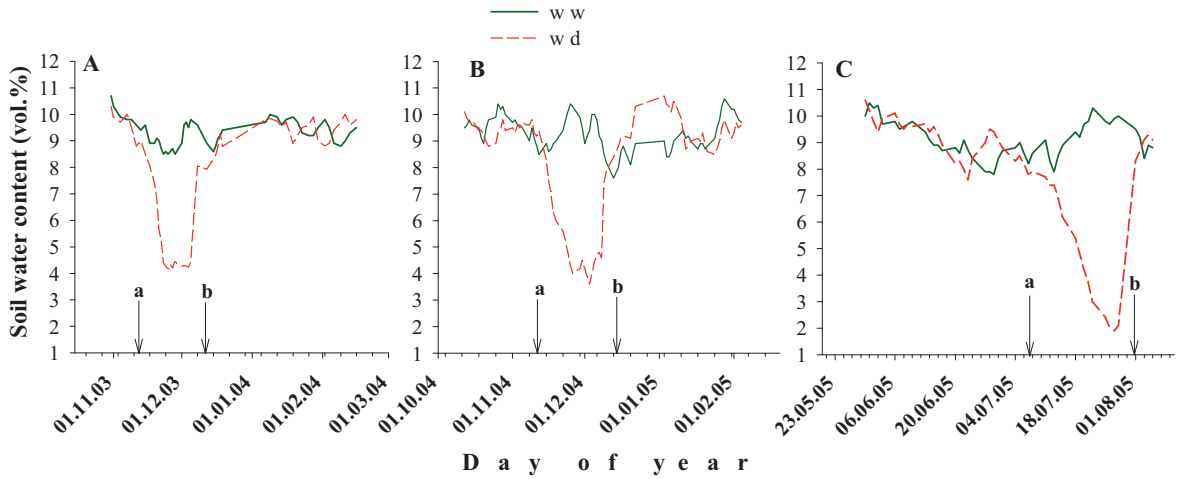

Fig. 5: Soil water content, SWC (vol. %) starting three weeks after planting to maturity in experiment 1 (**A**) and experiment 2 (**B**), or to the end of stress in experiment 3 (**C**) for the well-watered (ww) and water deficit (wd) treatments. Arrows **a** and **b** denote stress begin/onset of flowering and end of stress, respectively.

Soil water content (SWC) displayed a similar development to SWP; in fact there was a correlation betweeen SWC and SWP (R = 0,938 and 0,781 in Exp 1 and Exp 2, respectively; P ≤ 0,01), but only under wd conditions. In all three experiments, all pots had high SWC (9,0 – 11.0 %) before stress was imposed (Fig. 5). During stress, the wd treatment had a SWC of around 4,0 – 5,0 %, 4,0 – 4,5%, and 3,0 – 3,5% in Exp 1, Exp 2 and Exp 3, respectively. During the stress period in all experiments SWC of the ww treatment was kept between 8,0 and 11,0 %.

4.2. Gas exchange

4.2.1. Net photosynthetic rate (P_N)

On average, net photosynthetic rate (P_N) of the continuously irrigated (well-watered, ww) treatment was highest in Exp 2 (Fig. 6) before stress, but P_N at stress end (se) and rewatering (rew) was highest in Exp 1. Water deficit (wd) stress led to considerable decline of P_N in the three experiments, 61% in Exp 1, 42% in Exp 2 and 38% in Exp 3. In all experiments rewatering resulted in an improvement of P_N to levels similar to those of the ww treatment, with P_N of wd treatment in Exp 3 attaining a level even higher than that of ww treatment after rewatering. This shows that P_N recovered fully from the wd stress.

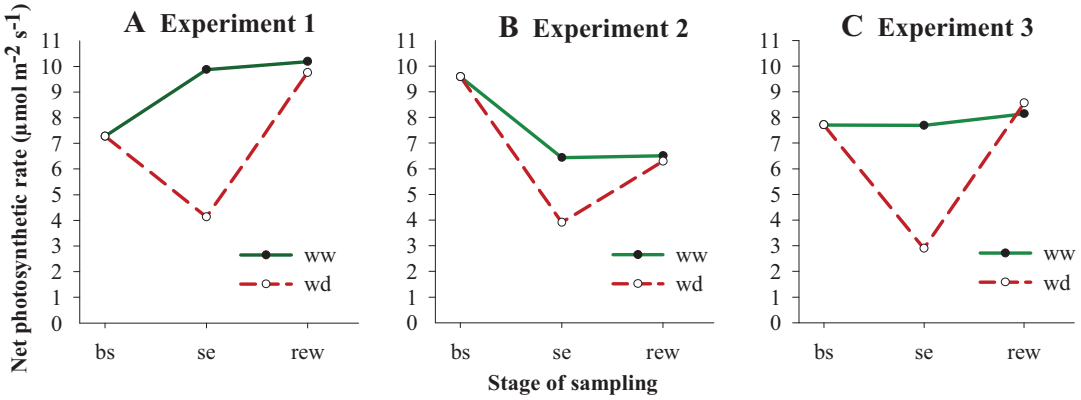

Fig. 6: Effect of water supply (well watered, ww and water deficit, wd) on mean net photosynthetic rate (P_N) at three dates (one day before stress, bs – also onset of flowering; stress end, se – at the point of maximum stress, and rewatering, rew – i. e. measurements carried out four days after resumption of full continuous irrigation) during three experiments.

Significant differences existed among genotypes for P_N (Table A1, Appendix) under ww and water wd conditions and at the different sampling dates (before stress, bs and at stress end, se – maximum stress level and rewatering, rew). No gas exchange measurements were undertaken before stress for Lagreen in Exp 2 because it had been sprayed with an insecticide upon which most of its plants showed a necrotic reaction on the leaves.

For most of the genotypes P_N was not consistent in the three experiments, whereby P_N was generally higher in Exp 1 than in the other two experiments. UCR 386 showed a similar trend of P_N in the first two experiments, displaying very high P_N bs (18,3 and 20,3 µmol m^{-2} s^{-1}) and then going down at the later sampling dates. The P_N trend of UCR 386 was different in the last experiment.

Water deficit stress led to reductions of P_N which ranged from 27% (UCR 1340) to 90% (Ex Ukwala) in Exp 1, 10% (IFH 27-8) to 66% (Ex Ukwala) in Exp 2 and 36% (Vita 7) to 73% (UCR 386) in Exp 3. Resumption of full irrigation improved the P_N of all wd plants (measured four days after resumption of full irrigation), such that P_N was as high as that of ww plants in all genotypes in the first two experiments or slightly higher in the case of Exp 3. Four days after resumption of full irrigation (rew) UCR 386 still had very low P_N of 4,7 µmol m^{-2} s^{-1} in Exp 1 and Exp 2.

4.2.2. Transpiration rate (E)

While, on average, transpiration rate (E) before stress (bs) was higher in Exp 2 and Exp 3 than in Exp 1, E was highest in Exp 3 at se and after rewatering (Fig. 7). Only in Exp 1 did E show a similar pattern as P_N, while the E trend was similar in Exp 1 and Exp 3 under ww conditions. E was clearly reduced by drought stress (Fig. 7).

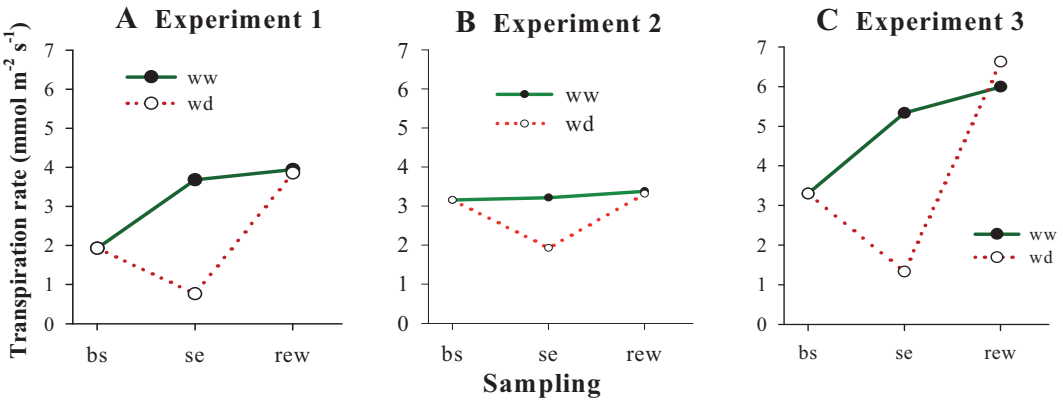

Fig. 7: Effect of water supply (well watered, ww and water deficit, wd) on genotypic mean transpiration rate (E) at three dates (one day before stress, bs – also onset of flowering; stress end, se – at the point of maximum stress, and rewatering, rew – i. e. measurements carried out four days after resumption of full continuous irrigation) during three experiments.

E under wd stress at se was lower in Exp 1 and Exp 3 than Exp 2, but after rewatering it was highest in Exp 3. Mean E declined by 79% in Exp 1, 40% in Exp 2 and 25% in Exp 3. The

relative reduction of E under wd stress was higher than that of P_N in the first two experiments, whereas mean P_N in Exp 3 experienced a higher reduction than E. Rewatering restored E to levels of the ww treatment.

Transpiration rate (E) showed genotypic variation in the different treatments and at different sampling dates in all three experiments (Table A2). Generally, E before stress was higher in Exp 2 than in Exp 1; higher bs than in the ww (se) treatment in Exp 2, but higher in ww (se) than before stress in Exp 1. Under continuous full irrigation (ww), E was generally higher in Exp 1, except Lagreen with a 100% higher E in Exp 2. E under wd stress declined in all genotypes of all experiments, such that E was reduced by 62 % (UCR 328) to 95 % (Ex Ukwala) in Exp 1, 22 % (Vita 7) to 73 % (Ex Ukwala) in Exp 2 and 43 % (Vita 7) to 87 % (UCR 386) in Exp 3. Ex Ukwala had the lowest E and largest E reduction in the first two experiments, contrary to UCR 328 that among the genotypes with the highest E and lowest E reduction in these two experiments. In Exp 3 Lagreen had the lowest E and Vita 7 the highest, while UCR 328 and UCR 386 underwent the highest reduction of E under wd stress. UCR 328 and UCR 1340 were the only genotypes displaying similar values under wd in Exp 1 and Exp 2. Stress led to a change in the ranking for E in the three experiments. Resumption of full irrigation ameliorated E and restored it to similar levels of the ww treatment in all experiments.

4.2.3. Stomatal conductance (g_s)

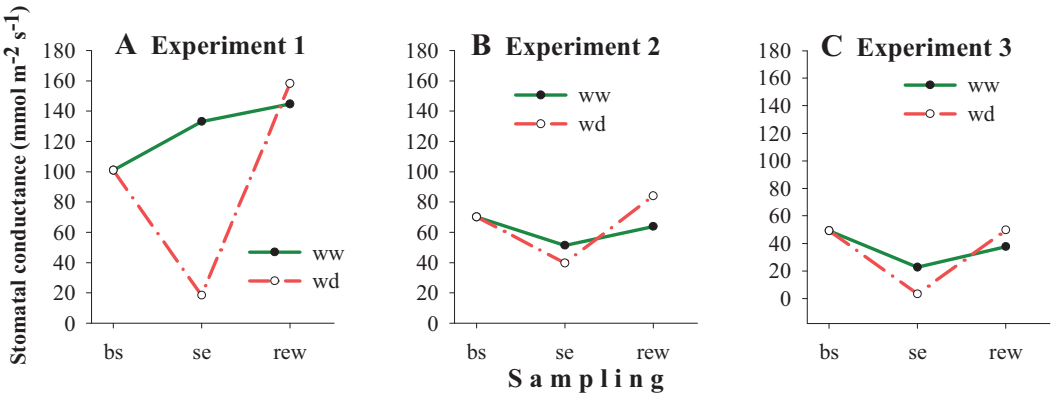

Fig. 8: Mean stomatal conductance for CO_2 (g_s) as influenced by water availability – one day before stress (bs)/onset of flowering, at maximum stress (se) and four days after resumption of full irrigation (rew)

Before stress (bs) mean stomatal conductance for CO_2 (g_s) (Fig. 8) was highest in Exp 2 and lowest in Exp 3. Mean stomatal conductance was lowest in Exp 3 at all sampling dates (Fig.

8). In Exp 2 g_s was lower than in Exp 1 at all sampling dates. There was no consistency among genotypes in all experiments. Only g_s in Exp 1 displayed a clearly similar pattern to that of P_n and E. Under water deficit conditions g_s declined relative to the ww treatment in all experiments. However, the decline was more pronounced in Exp 1 and Exp 3 (reduction by 86%) than in Exp 2 (reduction by 23%).

In Exp 1 and Exp 2 before stress, g_s (Table A3) had comparable values. At that sampling date in Exp 1, UCR 386 was the only genotype with a much higher g_s of 253 mmol m^{-2} s^{-1}. Under ww (se) conditions g_s was generally lower than before stress in both experiments, except TVu 12348 in Exp 2 which had a slightly higher g_s at ww (se). UCR 386 displayed an extremely low g_s value of 22 mmol m^{-2} s^{-1} (from 253 mmol m^{-2} s^{-1}, bs).

Water deficit stress reduced g_s in all experiments to such an extent that in Exp 1 g_s of Ex Ukwala, Lagreen, UCR 328 and IT 18 was reduced by, respectively, 98, 89, 85 and 81% compared to values under ww (se). The other two genotypes had g_s reduced by 43%. In Exp 2 under stress, Vita 7 (200%) and IFH 27-8 (72%) had much higher g_s, while particularly Ex Ukwala (83% reduction) and UCR 328 (80% reduction) much lower g_s than in the control (se) treatment. Rewatering restored g_s in both experiments.

4.2.4. Intrinsic transpiration efficiency (TE_i)

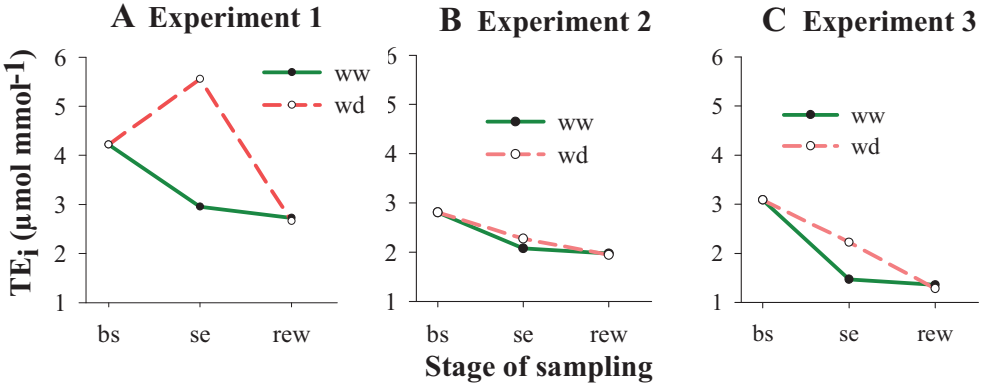

Fig. 9: Mean intrinsic transpiration efficiency (TE_i) over all genotypes before stress (bs), maximum stress (se) and four days after resumption of full irrigation (rew)

The intrinsic transpiration efficiency (TE_i), the amount of CO_2 which the leaf fixes for every unit of water transpired at any particular instant (that is P_N/E), was very high (Fig. 9) in experiment 1 (2,7 to 5,6 µmol CO_2 $mmol^{-1}$ H_2O) but lower and similar in Exp 2 (1,9 to 2,8

µmol CO_2 $mmol^{-1}$ H_2O) and 3 (1,5 to 3,1 µmol CO_2 $mmol^{-1}$ H_2O). In all experiments TE_i was higher under wd stress than in the control treatment, but more so in Exp 1 and Exp 3 than in Exp 2.

There were differences among genotypes for TE_i (Table A4) at the different sampling dates and in the two treatments. In the second experiment TE_i (bs) of three genotypes was, on the one hand, 22 to 43% of that in Exp 1 (bs) and TE_i (bs) of two genotypes, on the other hand, was higher in Exp 2 than in Exp 1. IT 18 alongside IFH 27-8 (1.5 µmol $mmol^{-1}$) had the lowest TE_i in Exp 2 before stress. Relating TE_i (bs) and TE_i (ww, se) in Exp 1 to that in Exp 2 showed that it was generally higher in the former. TE_i before stress varied from 1,8 (UCR 1340) to 6,7 (IT 18) µmol $mmol^{-1}$ (Exp 1) and 1,5 (IFH 27-8 and IT 18) to 5,7 (UCR 1340) µmol $mmol^{-1}$ (Exp 2), while under ww (se) conditions it ranged from 2,2 (Ex Ukwala) to 4,6 (UCR 386) µmol $mmol^{-1}$ (Exp 1), 1,7 (UCR 1340) to 2,8 µmol $mmol^{-1}$ (UCR 386) in Exp 2 and 1,1 (UCR 386) to 2,3 µmol $mmol^{-1}$ (IFH 27-8) in Exp 3. UCR 386 displayed an outstandingly high TE_i of 4,6 µmol $mmol^{-1}$ under ww (se) in Exp 1, reflecting the high P_N and g_s it had at that stage. Compared with Exp 1 only Ex Ukwala and UCR 328 maintained their TE_i at similar levels under ww (se) conditions in Exp 2, while all other genotypes in Exp 2 performed poorly in terms of TE_i.

Significantly higher TE_i under wd was obtained compared with TE_i under ww conditions. Water deficit (wd) stress led to a shift in the genotypic ranking for TE_i compared to TE_i before stress and under control conditions (se) in both experiments. Only UCR 328 remained at the same position. In Exp 1 the highest TE_i under wd stress was obtained for UCR 386 (also highest TE_i under ww (se) conditions) and Lagreen had the lowest TE_i under wd stress. Transpiration efficiency (TE_i) under drought stress in Exp 1 was 65 – 127% higher than in control treatment. In Exp 2 drought caused a decline of TE_i in Vita 7 (19%) and UCR 328 (17%), while TE_i increased slightly in IT 18 and TVU 12348 (both 6%). The remaining genotypes in Exp 2 experienced a rise in TE_i between 16 and 30% relative to ww (se) values. UCR 386 again had the highest TE_i under wd stress; it was among the genotypes with the highest TE_i before stress. In Exp 3, stress raised TE_i in all genotypes, the highest and lowest gains in TE_i occuring in UCR 328 (136%) and IFH 27-8 (2%), respectively. Under wd stress in this experiment, the TE_i of all the other genotypes was higher than that under ww conditions by 12% to 101%. Comparing experiments, UCR 328 and UCR 386 showed some

consistency for TE_i in the three experiments, while IFH 27-8 was consistent at the different sampling dates in Exp 3, being constantly among those with the highest TE_i.

TE_i four days after resumption of full irrigation declined compared with ww (se) levels in all genotypes and the ranking was surprisingly close to that under wd stress in Exp 1. TE_i of wd plants after rewatering was lower than that obtained under wd conditions. Comparing to Exp 1, TE_i under all treatments and sampling dates was lower in Exp 2, but most clearly under water deficiency. In Exp 3, the experiment was conducted only up to the end of stress, where all plants were subsequently destructively sampled.

4.2.5. Ratio of photosynthetic rate to stomatal conductance (P_N/g_s)

The ratio of P_N to g_s, henceforth referred to as P_N/g_s (µmol CO_2 $mmol^{-1}$ H_2O), a parameter which has been used by some researchers (Martin and Ruiz-Torres, 1992; Flexas *et al.*, 2006a; Flexas *et al.*, 2004; Jones, 2004) as the "real" intrinsic transpiration efficiency (TE_i), indicates that P_N/g_s in the control treatment at stress end compared with P_N/g_s (bs) declined by 8 and 56% in IT 18 and Ex Ukwala, respectively, as opposed to the partly huge increases (114 – 557%) in UCR 328, Lagreen, UCR 386 and UCR 1340 in Exp 1. In Exp 2 P_N/g_s (bs) was higher than (Ex Ukwala, UCR 1340 and UCR 386), lower than (IT 18) and in the other genotypes similar to that in Exp 1 (bs). P_N/g_s of TVu 12348 under ww (se) was slightly below one third of that found before stress and UCR 328 remained comparably stable between these two sampling dates.

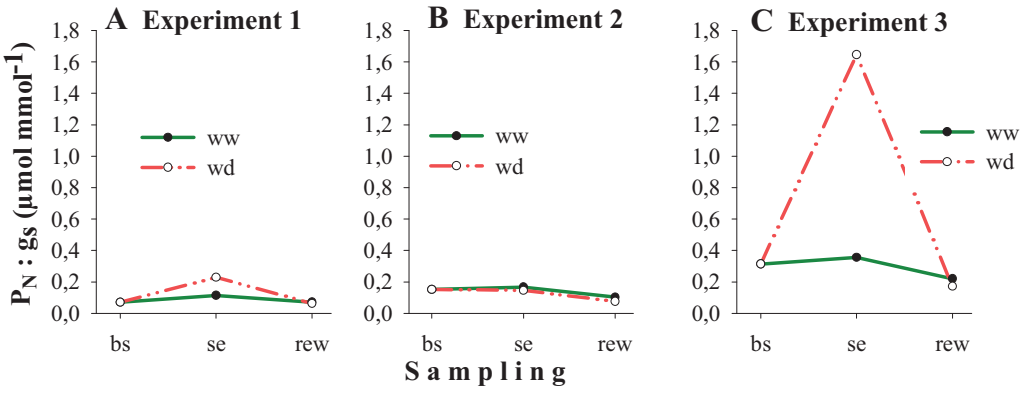

Fig. 10: Mean ratio of net photosynthetic rate (P_N) to stomatal conductance (g_s), P_N/g_s, over all genotypes before stress (bs), maximum stress (se) and four days after resumption of full irrigation (rew)

In Exp 3, P_N/g_s went down by 65% in Lagreen and by 37% in Vita 7 at ww (se) compared to that bs, while the rest had an increase ranging from 1% to 460%.

P_N/g_s increased (114 – 454%) under wd stress relative to the ww (se) in all genotypes in Exp 1. However, the absolute P_N/g_s under wd was computed for UCR 328 (0,436 µmol $mmol^{-1}$) and the lowest in IT 18, Ex Ukwala and UCR 1340 (Table A5). Contrary to Exp 1, wd stress in Exp 2 resulted in a mixed picture for P_N/g_s. Only three genotypes (Lagreen, Ex Ukwala and UCR 328) increased their P_N/g_s due to wd stress by 1 – 287%. The P_N/g_s of the other genotypes decreased by 26 – 48% compared with ww (se) treatment. In the third experiment, Pn/gs declined only in IFH 27-8 (13%), while wd stress gave rise to increments in all the other genotypes (30 – 963%).

4.3. Plant water status and water use

4.3.1. Leaf relative water content (RWC)

Genotype	**Experiment 1:** RWC (%)			**Experiment 2:** RWC (%)		
	ww (bs)	**ww (se)**	**wd (se)**	**ww (bs)**	**ww (se)**	**wd (se)**
Ex Ukwala	91,93 **c**	87,59 **a**	70,18 **c**	86,47 **cd**	77,47 **b**	65,86 **abc**
UCR 328	95,26 **d**	93,05 **c**	82,19 **d**	93,25 **e**	85,45 **d**	74,49 **d**
UCR 1340	84,11 **b**	81,54 **a**	67,26 **b**	79,51 **ab**	70,06 **a**	59,86 **a**
IT 18	91,18 **c**	88,86 **a**	70,54 **c**	88,56 **cde**	80,49 **bc**	63,08 **ab**
UCR 386	79,63 **a**	79,03 **a**	69,51 **a**	75,49 **a**	69,83 **a**	62,34 **ab**
Lagreen	92,77 **cd**	89,67 **b**	75,45 **c**	90,27 **de**	82,33 **cd**	69,89 **cd**
Vita 7	-	-	-	85,77 **cd**	77,97 **bc**	66,63 **bc**
TVu 12348	-	-	-	84,20 **bc**	76,04 **b**	70,77 **cd**
IFH 27-8	-	-	-	93,93 **e**	86,40 **d**	72,06 **cd**
Mean	**89,15**	**86,62**	**72,52**	**86,38**	**78,45**	**67,22**

Table 6: Leaf relative water content (RWC) under well-watered (ww) and water deficit (wd) conditions for experiment 1 and 2. Within each column, means followed by the same letter do not differ significantly at $P \leq 0,05$; n = 4 (experiment 1) and n = 6 (experiment 2) according to Duncan's Multiple Range Test (DMRT). bs: before stress; se: stress end (maximum wd stress)

In order to assess plant water status, leaf relative water content (RWC) was determined before stress (bs) and at the end of stress (se) . Before stress imposition in Exp 1, RWC varied from 79,6 (UCR 386) to 95,3 % (UCR 328) (Table 6), while it ranged from 75,5 (UCR 386) to 93,9 % (IFH 27-8) bs in Exp 2. Under well-watered (ww) conditions in both experiments, RWC was generally lower than bs, except UCR 386 in Exp 1 which remained at the same level. In comparison with Exp 1, RWC of the ww treatment in Exp 2 (Table 6) was relatively much lower than bs. In both experiments UCR 386 consistently had the lowest RWC, while UCR 328 (and also IFH 27-8 in Exp 2) always maintained the highest RWC. In Exp 2 under ww

conditions UCR 1340 also had the lowest RWC along with UCR 386. Under wd conditions in Exp 1, RWC was lower than under ww conditions, ranging between 67,3 (UCR 386) and 82,2% (UCR 328), being a drop in RWC between 9,5 (UCR 386) and 18,3 (IT 18) percentage points. Similar to the ww conditions, in absolute terms, UCR 386 again had the lowest RWC oppossed to UCR 328's highest RWC. However, the ranking had shifted slightly compared to that under ww conditions. Under wd conditions in Exp 2, RWC was reduced by a lower margin (5,3 to 17,4 %) compared to Exp 1, but the ranking was similar to that in this experiment under ww conditions, with UCR 328 maintaining the highest RWC while UCR 1340 and UCR 386 were also among those with the lowest RWC.

4.3.2. Water use (WU)

Up to seven days before onset of flowering (bs) all plants were watered manually in Exp 1 and 3, whereas in Exp 2 an automatic irrigation system was put to use already fifteen days after planting. Before stress (bs) each plant received, on average, 2,60, 2,88 and 2,54 L in Exp 1, Exp 2 and Exp 3, respectively.

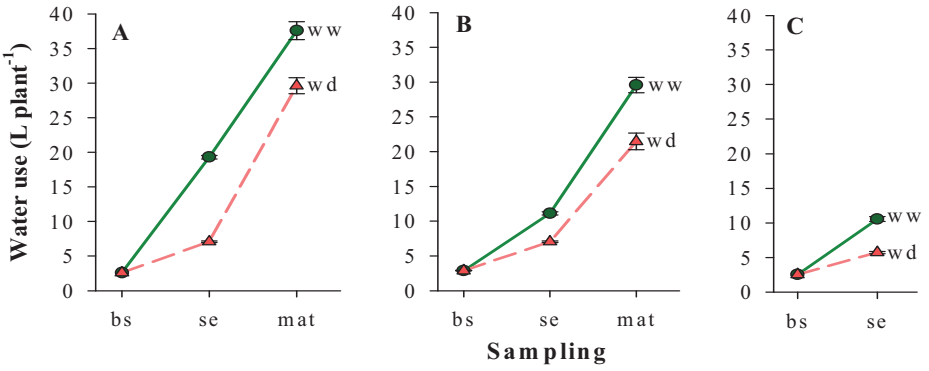

Fig. 11: Mean water utilised (L plant^{-1}) under well-watered (ww) and water deficit (wd) conditions at three dates (one day before stress, bs – also onset of flowering; stress end, se and maturity, mat – i. e. after all pods were harvested) during three experiments **A:** experiment 1, **B:** experiment 2 and **C:** experiment 3).

On average, in the well-watered (ww) treatment 19,30 and 37,61 L water plant^{-1} in Exp 1, and 11,13 and 29,58 L plant^{-1} in Exp 2 (Fig. 11) were used from planting to stress end (se) and from planting to maturity (mat), respectively, while in Exp 3 (where all plants were harvested immediately at se) 10,55 L plant^{-1} up to se were utilised. Under ww conditions, the intervals from planting to bs, bs-se and se-mat contributed 6,9, 44,4 and 48,7 % of total water use (WU) measured at maturity, respectively, in Exp 1, while it was 9,7, 27,9 and 62,4 % for the equivalent intervals in Exp 2. This affirms the differences in WU in the two experiments

under ww conditions, whereby mainly the relative WU of the interval bs-se in Exp 2 was very low, with a much higher relative WU in the interval se-mat. Nevertheless, both experiments hint at the fact that the importance of WU in the bs-se interval in determining total WU was relatively minor, more so in Exp 2. Ranking of genotypes for WU, notably at maturity, was similar in both experiments, with some slight variation in the three intervals.

In Exp 1 under ww conditions only two distinct groups (Table 7) could be identified, with Lagreen, UCR 1340 and UCR 328 having the higher WU. In Exp 2 and Exp 3, there was a greater variation among genotypes. In Exp 3, UCR 386 and TVu 12348 had the least WU and Ex Ukwala the highest. In Exp 3 UCR 328 had the least WU, less than 50 % of the highest WU (Lagreen).

As expected, the effect of water deficit (wd) stress manifested itself through a clear reduction of water uptake in all the experiments, but this reduction was highest in Exp 1. In the water deficit (wd) treatment, water use (WU) went down, on average, by 63,3, 36,8 and 45,8 % in Exp 1, Exp 2 and Exp 3, respectively, compared to WU in the ww treatment. At maturity, the overall mean WU of the wd treatment was 21,2 and 27,4 % lower than that of the ww treament in Exp 1 and 2, respectively. The relative contribution of the each of the three intervals to total WU was 8,8 % (planting-bs), 15,1 % (bs-se) and 76,1 (se-mat) in Exp 1 compared to 13,4, 19,4 and 67,2 % in Exp 2.

In the interval bs-se under wd conditions, water utilised was 21,8 to 31,7 % of the ww treatment in Exp 1. In Exp 2, WU of the wd treatment was 43,6 to 57,8 % of the ww treatment, values much higher than those in Exp 1. There was no clear consistency of genotypic ranking in both experiment. However, the genotypic ranking for WU of the se-mat interval was similar to that for the ww treatment with the exception of Lagreen in Exp 1 and UCR 1340 and Lagreen in Exp 2. In the wd treatment of Exp 1 and Exp 2, UCR 328 was among those with the lowest WU, while Ex Ukwala (which the highest WU in Exp 1) had an intermediate WU in Exp 2. Of the three additional genotypes in Exp 2, IFH 27-8 had low WU, TVu 12348 intermediate and Vita 7 high WU.

Genotype	***A*** well-watered (ww) treatment							
	Experiment 1			Experiment 2			Experiment 3	
	bs	**bs-se**	**se-mat**	**bs**	**bs-se**	**se-mat**	**bs**	**bs-se**
Ex U	2,60	15,27 **a**	29,82 **c**	2,96 **e**	12,28 **e**	23,60 **e**	-	-
U328	2,60	17,22 **b**	8,64 **a**	2,99 **f**	7,43 **b**	11,21 **a**	2,54	3,40 **a**
U1340	2,60	17,69 **b**	18,53 **b**	2,72 **d**	7,47 **b**	17,69 **bc**	2,54	8,34 **d**
IT18	2,60	15,78 **a**	16,92 **b**	3,08 **g**	8,15 **c**	13,59 **ab**	2,54	9,10 **e**
U386	2,60	16,12 **a**	20,02 **b**	2,65 **c**	6,7 **a**	22,53 **de**	2,54	9,68 **f**
Lag	2,60	18,13 b	15,91 **b**	2,63 **a**	8,87 **d**	19,26 **cd**	2,54	10,11 **g**
Vita 7	-	-	-	3,08 **h**	8,90 **d**	32,93 **f**	2,54	7,15 **b**
TVu	-	-	-	2,64 **b**	6,81 **a**	14,37 **ab**	-	-
IFH	-	-	-	3,13 **i**	7,60 **b**	10,91 **a**	2,54	8,28 **c**
Mean	**2,60**	**16,70**	**18,31**	**2,88**	**8,25**	**18,45**	**2,54**	**8,01**

Genotype	***B*** water deficit (wd) treatment							
	Experiment 1			Experiment 2			Experiment 3	
	bs	**bs-se**	**se-mat**	**bs**	**bs-se**	**se-mat**	**bs**	**bs-se**
Ex U	2,60	4,84 **d**	29,10 **c**	2,96 **e**	5,47 **i**	16,98 **c**	-	-
U328	2,60	3,76 **a**	17,24 **a**	2,99 **f**	4,30 **g**	6,26 **a**	2,54	1,16 **a**
U1340	2,60	4,95 **d**	18,47 **a**	2,72 **d**	3,96 **c**	4,63 **a**	2,54	3,34 **d**
IT18	2,60	4,79 **cd**	17,43 **a**	3,08 **g**	4,16 **e**	11,46 **b**	2,54	3,64 **e**
U386	2,60	4,26 b	28,82 **c**	2,65 **c**	2,95 **a**	19,05 **c**	2,54	3,87 **f**
Lag	2,60	4,30 **bc**	24,30 **b**	2,63 **a**	4,29 f	29,10 **e**	2,54	4,04 **g**
Vita 7	-	-	-	3,08 **h**	5,10 **h**	24,89 **d**	2,54	2,86 **b**
TVu	-	-	-	2,64 **b**	3,12 **b**	11,70 **b**	-	-
IFH	-	-	-	3,13 **i**	4,10 **d**	5,82 **a**	2,54	3,31 **c**
Mean	**2,60**	**4,48**	**22,56**	**2,88**	**4,16**	**14,43**	**2,54**	**3,18**

Table 7: The amount of water used plant^{-1} in the intervals planting to flowering onset (bs), before stress to stress end (bs – se) and from stress end to maturity (se – mat) in Exp 1 (N = 4 plants per genotype), Exp 2 (N = 6 plants per genotype) and Exp 3 (N = 5 plants per genotype) in the well-watered (ww), ***A*** and water deficit (wd), ***B*** treatments. Within each column, means followed by the same letter do not differ significantly at P ≤ 0,05 according to Duncan's Multiple Range Test (DMRT).

	Exp 1: WU (L plant^{-1})		**Exp 2:** WU (L plant^{-1})	
	0-mat (ww)	**0-mat (wd)**	**0-mat (ww)**	**0-mat (wd)**
Ex Ukwala	47,69 ± 2,78 **c**	36,54 ± 1,71 **c**	38,84 ± 1,29 **d**	25,40 ± 1,17 **c**
UCR 328	28,46 ± 0,80 **a**	23,60 ± 1,02 **a**	21,63 ± 0,37 **a**	13,55 ± 0,58 **a**
UCR 1340	38,82 ± 0,86 **b**	26,02 ± 0,44 **a**	27,87 ± 1,65 **bc**	11,30 ± 1,19 **a**
IT 18	35,30 ± 0,43 **b**	24,82 ± 0,77 **a**	24,82 ± 1,19 **a**	18,69 ± 0,99 **b**
UCR 386	38,74 ± 0,63 **b**	35,68 ± 1,16 **c**	31,94 ± 2,03 **bc**	24,65 ± 1,57 **c**
Lagreen	36,63 ± 1,74 **b**	31,20 ± 0,83 **b**	30,76 ± 0,97 **c**	36,02 ± 1,52 **d**
Vita 7	**-**	**-**	44,91 ± 2,18 **e**	33,08 ± 0,95 **d**
TVu 12348	**-**	**-**	23,81 ± 0,85 **ab**	17,46 ± 0,72 **b**
IFH 27-8	**-**	**-**	21,64 ± 0,62 **a**	13,06 ± 0,88 **a**
Mean	**37,61 ± 1,30**	**29,64 ± 1,14**	**29,58 ± 1,12**	**21,47 ± 1,20**

Table 8: Total water use (WU) at maturity, i. e. from planting to maturity (0-mat), (means ± standard error) for well-watered (ww) and water deficit (wd) treatments for experiment 1 and 2. Within each column, means followed by the same letter do not differ significantly at P ≤ 0,05; N = 4 (experiment 1) and N = 6 (experiment 2) according to Duncan's Multiple Range Test (DMRT).

4.3.3. Evapotranspiration efficiency (ETE)

Evapotranspiration efficiency (ETE) is the amount of shoot biomass (DM) accumulated for every unit of water used (g DM L^{-1} H_2O). Evapotranspiration efficiency (ETE) before stress (bs), on average, was 2,7, 1,1 and 0,8 g L^{-1} in Exp 1, Exp 2 and Exp 3, respectively (Table 9). In Exp 1 ETE bs was higher than the values determined during stress, in Exp 2 at this sampling date ETE was lowest compared to later dates, and in Exp 3 it was only higher than that under ww conditions. Under ww conditions, ETE averaged 2,3 (Exp 1), 1,3 (Exp 2) and 0,7 g L^{-1} (Exp 3). There was variation among genotypes in all experiments (Table 9), with ETE extending between 2,1 g L^{-1}

Genotype	Experiment 1: ETE (g L^{-1})			Experiment 2: ETE (g L^{-1})			Experiment 3: ETE (g L^{-1})		
	bs	**ww**	**wd**	**bs**	**ww**	**wd**	**bs**	**ww**	**wd**
Ex Ukwala	3,00c	2,11a	2,39c	1,43bc	0,86a	1,57b	-	-	-
UCR 328	2,24a	2,45b	2,63d	1,56c	1,56c	1,12ab	0,72ab	0,96c	1,25c
UCR 1340	2,60abc	2,32b	2,04a	0,83ab	1,28abc	0,68a	0,85bc	0,73b	0,88b
IT 18	2,92bc	2,13a	2,22b	1,08abc	1,61c	0,72a	0,82bc	0,51b	0,87ab
UCR 386	2,55ab	2,40b	2,24b	1,19abc	1,39bc	1,64b	0,63a	0,47a	0,73a
Lagreen	2,63abc	2,39b	2,47c	0,54a	0,94ab	0,77a	1,12d	0,72b	1,17c
Vita 7	-	-	-	0,99abc	1,11abc	1,10ab	0,98cd	0,65b	0,96b
TVu 12348	-	-	-	1,14abc	1,19abc	2,88c	-	-	-
IFH 27-8	-	-	-	0,96abc	1,40bc	1,68b	0,72ab	0,71b	0,91b
Mean	**2,65**	**2,30**	**2,33**	**1,08**	**1,26**	**1,35**	**0,83**	**0,68**	**0,97**

Table 9: Evapotranspiration efficiency (ETE) under well-watered (ww) and water deficit (wd) conditions for Exp 1 (N = 4), Exp 2 (N = 6) and Exp 3 (N = 5) at bs (0-bs) and se (0-se). Means of genotypes followed by the same letter are not significantly different within an experiment and column ($P \leq 0,05$; Duncan's Multiple Range Test).

(UCR 1340 and IT 18) and 2,5 g L^{-1} (UCR 328) in Exp 1, from 0,9 g L^{-1} (Ex Ukwala and Lagreen) to 1,6 g L^{-1} (UCR 328 and IT 18) in Exp 2 and from 0,5 g L^{-1} (UCR 386 and IT 18) to 1,0 g L^{-1} (UCR 328) in Exp 3. The genotypic ranking was not similar to that bs, except for UCR 1340 intermediate in Exp 1 and Exp 3; Lagreen intermediate in Exp 1, but low in Exp 2 and UCR 386 in Exp 2 remaining at intermediate to high, but low in Exp 3.

Under water deficit conditions (wd) ETE was generally higher than under ww conditions, specifically exhibiting means of 2,3 g L^{-1} in Exp 1, 1,4 g L^{-1} in Exp 2 and 1,0 g L^{-1} in Exp 3 (Table 9). This was, on avarage, a constant ETE in Exp 1 (an improvement of only 1 %), an increase in Exp 2 (7 %) and a pronounced upsurge in Exp 3 (43 %). There was variation among genotypes in all three experiments under wd conditions (Table 9), with ETE varying between 2,0 g L^{-1} UCR 1340) and 2,6 g L^{-1} (UCR 328) in Exp 1, 0,7 g L^{-1} (UCR 1340 and IT 18) and 2,9 g L^{-1} (TVu 12348) in Exp 2 and 0,7 g L^{-1} (UCR 386) and 1,3 g L^{-1} (UCR 328) in

Exp 3. In the first two experiments, some genotypes had a higher ETE, some remained constant, yet others had a lower ETE under wd stress. In Exp 1, Lagreen (3 %), IT 18 (4 %), UCR 328 (7 %) and Ex Ukwala (13 %) increased their ETE, while UCR 386 (7 %) and UCR 1340 (12 %) reduced theirs. In Exp 2, Vita 7 remained constant, while TVu 12348 (142 %), Ex Ukwala (83 %), IFH 27-8 (20 %) and UCR 386 (18 %) increased their ETE. Lagreen (18 %), UCR 328 (28 %), UCR 1340 (47 %) and IT 18 (55 %) reduced their ETE under wd conditions. In Exp 3, all genotypes had a higher ETE under wd stress than under ww conditions. The increase ranged from 20 % (UCR 1340) to 70 % (IT 18). This result demonstrates that there is no clear consistency in the behaviour of ETE in the three experiments. The genotypic ranking differed between wd and ww conditions, particularly in the first two experiments. However, UCR 328 (high ETE), IT 18 (low ETE) and Lagreen (intermediate ETE) in Exp 1, UCR 328 (high ETE), UCR 386 (intermediate ETE) and Lagreen (low ETE) in Exp 2 (excluding the three additional genotypes) remained at similar positions in both treatments. Two of the three additional genotypes were relatively stable (Vita 7, intermediate; IFH 27-8, high) while TVu 12348 flactuated from intermediate (ww) to high (wd). In Exp 3, the genotypic ranking under wd stress was largely similar to that under ww conditions, with the exception of UCR 1340 and Vita 7 which flactuated. In the latter experiment, UCR 328, Lagreen and IFH 27-8 consistently had high ETE, while UCR 386 and IT 18 consistently had low ETE, and UCR 1340 as well as Lagreen displayed intermediate ETE. This result confirms some results of the two preceding experiments, namely that UCR 328 generally is a high ETE genotype, Lagreen intermediate and IT 18 low.

At maturity, ETE was determined only in Exp 1 and 2. The ww treatment in Exp 1 had, on average, 3,4 g L^{-1} and in Exp 2 0,9 g L^{-1} (Table 10). As at the sampling dates before maturity, there was variation of ETE among genotypes in both experiments, whereby ETE varied between 3,0 g L^{-1} (IT 18) and 3,9 g L^{-1} (Ex Ukwala and UCR 328) in Exp 1 and between 0,7 g L^{-1} (TVu 12348) and 1,0 g L^{-1} (UCR 328, Ex Ukwala and Vita 7) in Exp 2. The rankings were not similar to those at the previous sampling dates.

On average, the wd treatment had a higher ETE (3,7 g L^{-1}) than that of the ww treatment and at the previous sampling dates in Exp 1, while the ETE in Exp 2 was lower (0,9 g L^{-1}) than that at the previous sampling dates but only slightly higher than that of the ww treatment at maturity. As expected, there was also variation among genotypes in the wd treatment and a shift in the ranking of genotypes for ETE in the two experiments. In Exp 1, IT 18 (3,0 g L^{-1})

had the lowest ETE while UCR 328 (4,1 g L^{-1}) and UCR 386 (4,2 g L^{-1}) had the highest ETE. The ETE of genotypes was generally higher in the wd than the ww treatment, except Ex Ukwala (7 % lower) and IT 18 (only marginally higher at 2 %). In Exp 2, it was again IT 18 (0,6 g L^{-1}) with the lowest ETE and IFH 27-8, Ex Ukwala and Vita 7 (1,2 g L^{-1}) had the highest ETE in the wd treatment at maturity. Although UCR 328 did not hat the highest ETE, it was among those with the highest (1,1 g L^{-1}). In Exp 2, some genotypes had lower (UCR 1340, 26 %; IT 18, 32 %; Lagreen, 21 %) ETE than that of the ww treatment others higher (UCR 328, 6 %; Ex Ukwala, 17%; Vita 7, 18 %; TVu 12348, 24 %; UCR 386, 26 %; IFH 27-8, 44 %). It is interesting to note that in both experiments in the wd treatment, UCR 328 had an ETE which was 7 % and 6 % (very close values) higher than in the ww treatment.

Genotype	Experiment 1: ETE (g L^{-1})		Experiment 2: ETE (g L^{-1})	
	0-mat (ww)	0-mat (wd)	0-mat (ww)	0-mat (wd)
Ex Ukwala	3,878±0,073c	3,616±0,185b	1,017±0,025d	1,190±0,057d
UCR 328	3,795±0,374c	4,058±0,056c	1,012±0,030d	1,075±0,044cd
UCR 1340	3,187±0,081ab	3,613±0,028b	0,907±0,063bcd	0,671±0,115ab
IT 18	2,975±0,027a	3,025±0,056a	0,935±0,043cd	0,632±0,040a
UCR 386	3,535±0,060bc	4,226±0,139c	0,782±0,030ab	0,985±0,131cd
Lagreen	3,270±0,100ab	3,564±0,067b	0,855±0,053bc	0,677±0,034ab
Vita 7	-	-	1,023±0,035d	1,203±0,032d
TVu 12348	-	-	0,715±0,045a	0,887±0,047bc
IFH 27-8	-	-	0,818±0,039abc	1,174±0,135d
Mean	**3,440**±0,091	**3,684**±0,089	**0,896**±0,019	**0,944**±0,039

Table 10: Evapotranspiration efficiency, ETE (means ± standard error) at maturity for the well-watered (ww) and water deficit (wd) treatments for Exp 1 (N = 4) and Exp 2 (N = 6). Means of genotypes followed by the same letter are not significantly different within an experiment and column ($P \leq 0.05$; Duncan's Multiple Range Test).

4.3.3.1. Evapotranspiration efficiency (ETE) during stress intervals

The ETE during the intervals (planting, 0 to one day before stress, bs – i. e. 0-bs; bs to stress end, se – i.e. bs-se; and se to maturity, mat – i.e. se-mat) is presented here in order to assess the behaviour of the genotypes in the three intervals in the two treatments. In estimating the ETE of cowpeas the approach of using the interval ETE is appropriate in order to evaluate the actual ETE during the stress period only, hence eliminating the bias that could arise in ETE as a result of the DM produced before stress.

Mean ETE under ww conditions during the intervals was 2,65 g DM L^{-1} water (0-bs), 1,95 g L^{-1} (bs-se) and 4,95 g L^{-1} (se-mat) in Exp 1; 1,08 g L^{-1} (0-bs), 0,87 g L^{-1} (bs-se) and 0,85 g L^{-1}

(se-mat) in Exp 2 and 0,83 g L^{-1} (0-bs) and 0,64 g L^{-1} (bs-se) in Exp 3 (Table 11A). With that ETE was generally higher in Exp 1 than in the two subsequent experiments. In the intervals bs-se and se-mat UCR 328 had the highest ETE, while IT 18 had the lowest in both intervals in Exp 1 (Table 11A). In Exp 2, UCR 328 was among genotypes with the highest ETE and TVu 12348 was among those with the lowest ETE in the intervals bs-se and se-mat. Genotypic ranking for ETE was not consistent in the three experiments.

Under wd conditions, mean ETE was 2,84 g L^{-1} (bs-se) and 4,12 g L^{-1} (se-mat) in Exp 1, 0,71 g L^{-1} (bs-se) and 1,08 g L^{-1} (se-mat) in Exp 2 and 1,13 g L^{-1} (bs-se) in Exp 3 (Table 11B). Similar to ww conditions, ETE under wd conditions was conspicuously higher in Exp 1 than in the ensuing experiments.

	A ETE, ww							
	Experiment 1			Experiment 2			Experiment 3	
Genotype	**0-bs**	**bs-se**	**se-mat**	**0-bs**	**bs-se**	**se-mat**	**0-bs**	**bs-se**
Ex U	3,00 c	1,69 a	5,20 ab	1,43 bc	0,51 a	1,24 c	-	-
U328	2,24 a	2,15 b	5,66 b	1,56 c	0,94 ab	0,91 abc	0,72 ab	1,11 c
U1340	2,60 abc	2,03 b	4,57 a	0,83 ab	0,98 b	0,88 abc	0,85 bc	0,69 b
IT18	2,92 bc	1,68 a	4,37 a	1,08 abc	1,22 b	0,65 a	0,82 bc	0,42 a
U386	2,55 ab	2,07 b	5,00 ab	1,19 abc	0,92 ab	0,70 ab	0,63 a	0,42 a
Lag	2,63 abc	2,11 b	4,92 ab	0,54 a	0,78 ab	0,93 abc	1,12 d	0,60 ab
Vita 7	-	-	-	0,99 abc	0,77 ab	1,09 bc	0,98 cd	0,54 ab
TVu	-	-	-	1,14 abc	0,75 ab	0,61 a	-	-
IFH	-	-	-	0,96 abc	1,01 b	0,62 a	0,72 ab	0,69 b
Mean	**2,65**	**1,95**	**4,95**	**1,08**	**0,87**	**0,85**	**0,83**	**0,64**

	B ETE, wd							
	Experiment 1			Experiment 2			Experiment 3	
Genotype	**0-bs**	**bs-se**	**se-mat**	**0-bs**	**bs-se**	**se-mat**	**0-bs**	**bs-se**
Ex U	3,00 c	2,76 b	3,95 b	1,43 bc	0,80 ab	1,25 cd	-	-
U328	2,24 a	3,51 d	4,59 c	1,56 c	0,35 ab	1,57 d	0,72 ab	2,32 b
U1340	2,60 abc	2,46 a	4,26 bc	0,83 ab	0,13 a	1,03 bc	0,85 bc	0,89 a
IT18	2,92 bc	2,47 a	3,37 a	1,08 abc	0,30 ab	0,78 ab	0,82 bc	0,88 a
U386	2,55 ab	2,75 b	4,71 c	1,19 abc	0,92 b	1,02 bc	0,63 a	0,78 a
Lag	2,63 abc	3,07 c	3,88 b	0,54 a	0,47 ab	0,72 ab	1,12 d	1,17 a
Vita 7	-	-	-	0,99 abc	0,52 ab	1,37 cd	0,98 cd	0,84 a
TVu	-	-	-	1,14 abc	1,91 c	0,55 a	-	-
IFH	-	-	-	0,96 abc	0,97 b	1,44 cd	0,72 ab	1,03 a
Mean	**2,65**	**2,84**	**4,12**	**1,08**	**0,71**	**1,08**	**0,83**	**1,13**

Table 11: Evapotranspiration efficiency, ETE (g DM L^{-1} H_2O) in the intervals planting to flowering onset (0-bs), before stress to stress end (bs – se) and from stress end to maturity (se – mat) in experiment 1 (N = 4 plants per genotype), experiment 2 (N = 6 plants per genotype) and experiment 3 (N = 5 plants per genotype) in the well-watered (ww), ***A*** and water deficit (wd), ***B*** treatments. Same letters in a column show lack of difference ($P \leq 0,05$) among genotypes according to Duncan's Multiple Range Test.

ETE was higher in all genotypes by 21 – 63 % (Exp 1) and 49 – 110 % (Exp 3) than that under ww conditions. In Exp 2, it was higher only in Ex Ukwala (57 %) and TVu 12348 (155 %), constant in UCR 386 and lower (4 – 87 %) in all other genotypes. UCR 328 was generally among those with the highest ETE especially in the interval se-mat in Exp 1 and 2, while IT 18 and Lagreen were among those with the lowest ETE in both experiments. Under wd conditions, genotypic ranking was also not consistent among the intervals and three experiments.

4.3.4. Water-use efficiency (WUE)

Here water-use efficiency (WUE) is defined as the amount of DM of the economic product (grain yield) produced for every litre of water used by the plant.

As to be expected from the ETE data, WUE was much higher in Exp 1 than in Exp 2 in both treatments. In the ww treatment mean WUE was 1,0 g L^{-1} in Exp 1 compared to 0,2 g L^{-1} in Exp 2 (Table 12). In both experiments under ww conditions, there was variation among genotypes, WUE ranging from 0,1 g L^{-1} (Ex Ukwala) to 1,7 g L^{-1} (UCR 328) in Exp 1 and from 0,2 g L^{-1} (TVu 12348) to 0,5 g L^{-1} (UCR 328) in Exp 2.

	Experiment 1: WUE		**Experiment 2:** WUE	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	0,078 ± 0,017 **a**	0,011 ± 0,007 **a**	0,000 **a**	0,000 **a**
UCR 328	1,662 ± 0,143 **d**	1,817 ± 0,048 **d**	0,514 ± 0,017 **e**	0,471 ± 0,076 **c**
UCR 1340	1,025 ± 0,071 **b**	1,364 ± 0,111 **c**	0,289 ± 0,018 **c**	0,182 ± 0,028 **b**
IT 18	1,375 ± 0,031 **c**	1,346 ± 0,029 **c**	0,446 ± 0,027 **d**	0,185 ± 0,031 **b**
UCR 386	0,974 ± 0,046 **b**	0,907 ± 0,133 **b**	0,216 ± 0,030 **b**	0,100 ± 0,040 **ab**
Lagreen	1,083 ± 0,078 **b**	1,094 ± 0,038 **b**	0,281 ± 0,024 **c**	0,190 ± 0,019 **b**
Vita 7	-	-	0,000 **a**	0,000 **a**
TVu 12348	-	-	0,153 ± 0,017 **b**	0,184 ± 0,024 **b**
IFH 27-8	-	-	0,343 ± 0,039 **c**	0,461 ± 0,044 **c**
Mean	**1,033 ± 0,106**	**1,090 ± 0,120**	**0,249 ± 0,024**	**0,197 ± 0,025**

Table 12: Water-use efficiency (WUE) at maturity (means ± standard error) under well-watered (ww) and water deficit (wd) conditions for experiment 1 and 2. Same letters signify lack of difference among genotypes within an experiment and column ($P \leq 0,05$) according to Duncan's Multiple Range Test.

In the water deficit (wd) treatment, mean WUE was 1,1 g L^{-1} (6 % higher than in the ww treatment) in Exp 1 and 0,2 g L^{-1} (21 % lower than ww treatment) in Exp 2. There was variation among genotypes in both experiments and ranking of genotypes for WUE differed between wd and ww and experiments. However, UCR 328 had always the highest WUE in both experiments and treatments, while UCR 386 was always among the lowest. IT 18 had a

tendency to have a high WUE in the ww treatment but intermediate WUE in the wd treatment. In the wd treatment in Exp 1, UCR 1340 (33 %) and UCR 328 (9 %) had WUE higher than that in the ww treatment, while IT 18 (2 %), UCR 386 (7 %) and Ex Ukwala (86 %) lower than that of the ww treatment. Lagreen had WUE similar to that under ww conditions. In Exp 2 all genotypes common to both experiments had WUE lower than that of the ww treatment, while of the additional genotypes TVu 12348 and IFH 27-8 had WUE had WUE higher than that of their ww treatment. However, the reduction of WUE in the wd treatment in Exp 2 was minimal only in UCR 328.

The WUE results in both experiments and treatments underline UCR 328 (and possibly IFH 27-8 as well) as a genotype that has not only high WUE, but also high ETE under both treatments.

4.4. Growth and biomass allocation

4.4.1. Relative growth rate (RGR)

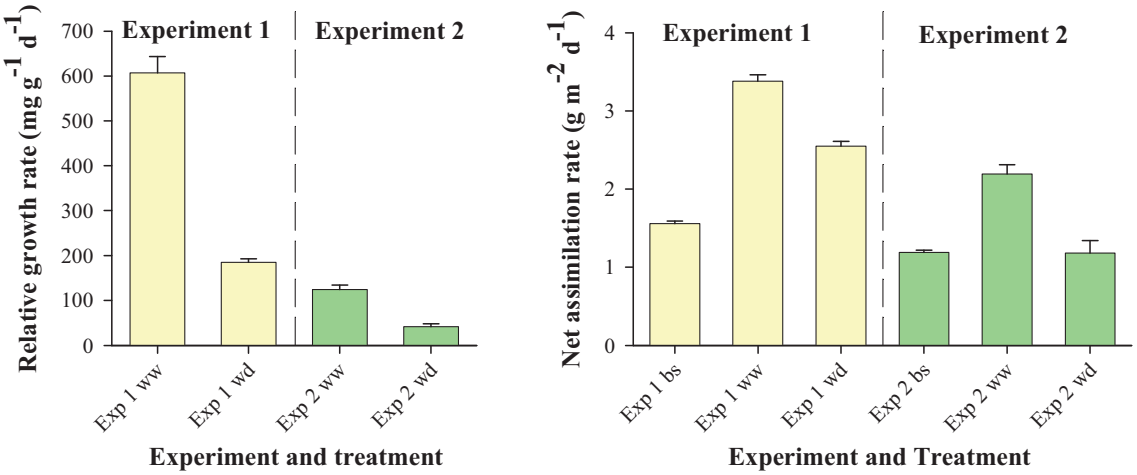

Fig. 12: Mean relative growth rate, RGR and mean net assimilation rate, NAR before stress (bs), as well as for the well-watered (ww) and water deficit (wd) treatments in Exp 1 and Exp 2

In the ww treatment in Exp 1, the mean RGR across all genotypes was 607 mg g^{-1} d^{-1} (Fig. 12 and Table A8). This was clearly much higher than that of Exp 2 (124 mg g^{-1} d^{-1}) (Fig. 12 and Table A8). In Exp 1, the RGR ranged from 417 (Ex Ukwala) to 777 mg g^{-1} d^{-1} (UCR 1340), whereas in Exp 2 it was 61 (Ex Ukwala) to 242 mg g^{-1} d^{-1} (Lagreen).

Water deficit (wd) stress led to a clear reduction of RGR in all experiments (Fig. 12 and Table A8). Compared to the ww treatment, wd stress brought about a decline in all experiments, the mean reduction being larger in Exp 1 (69 %) than in Exp 2 (66 %). In Exp 1, particularly UCR 328 and UCR 1340 had high RGR under both treatments. While Ex Ukwala and IT 18 had the lowest RGR under ww conditions, they also had the lowest RGR reduction of 60 and 66 %, respectively, under wd stress. All the other genotypes experienced the same level of reduction (71 %). In Exp 2 it was UCR 328, UCR 1340 and IT 18 with the lowest RGR. In Exp 2, again Ex Ukwala had the lowest decline (15 %) in RGR and TVu 12348 even had a rise (17 %). The rest had a very high reduction (47 – 94 %).

4.4.2. Net assimilation rate (NAR)

Net assimilation rate (NAR), the net shoot biomass gained by a plant for every unit of leaf area, did not show any variability among genotypes before stress (bs) in Exp 1 but variation existed under ww and wd conditions (Table A9), while NAR in Exp 2 varied among genotypes at all sampling dates and under both treatments. NAR in Exp 2 was lower as generally typified by the mean values (Table A9). In the ww treatment in Exp 1, NAR was highest in UCR 328 (4,0 g m^{-2} day^{-1}), while Ex Ukwala had the lowest (2,9 g m^{-2} day^{-1}). In Exp 2 the position of IT 18 was partially confirmed, having the highest NAR. Again Ex Ukwala was among those with the lowest NAR along with TVu 12348 under ww conditions in Exp 2.

NAR under stress declined in all genotypes in Exp 1, but in Exp 2 two genotypes had a higher NAR than in the control treatment. In the stress treatment in Exp 1 significant reduction of NAR (16 – 32%) occurred in all genotypes. UCR 328 was among those with the highest NAR in both treatments, but the reduction of its NAR under drought stress ranked among the highest (31%) as opposed to 16% reduction in IT 18. In Exp 2 under stress TVu 12348 (28%) and IFH 27-8 (14%) showed a higher NAR under wd stress. The other seven genotypes had reduction varying between 18 and 87%.

4.4.3. Main stem length and stem mass to length ratio

4.4.3.1. Main stem length

The main stem (Fig. 13) was longest in the ww (se) treatment, followed by the wd treatment and there was variation among genotypes in the three sampling categories (bs, ww and wd). UCR 328 had the shortest main stems before stress and also under ww (se) and wd (se) conditions and was the only genotype that remained at a particular rank in Exp 1 (Table A10). Main stem length in Exp 1 varied between 198 cm (UCR 328) and 317 cm (UCR 1340) under ww (se) conditions, and between 133 cm (UCR 328) and 220 cm (UCR 1340) under wd stress (Table A10). This means that UCR 1340 which had the longest stems under ww conditions also produced the longest stems under drought stress. Water deficit stress led to shorter stems (-17 to -37%) in all genotypes compared to the control treatment. In the second experiment there was variation among the genotypes at all sampling dates. Contrary to the results obtained in the first experiment, UCR 1340 had the shortest stems before stress and under stress, while UCR 386 had shortest stems throughout. Stems of Ex Ukwala were longest at both sampling dates. There was decline in stem length under drought ranging from only 5% to as much as 74%.

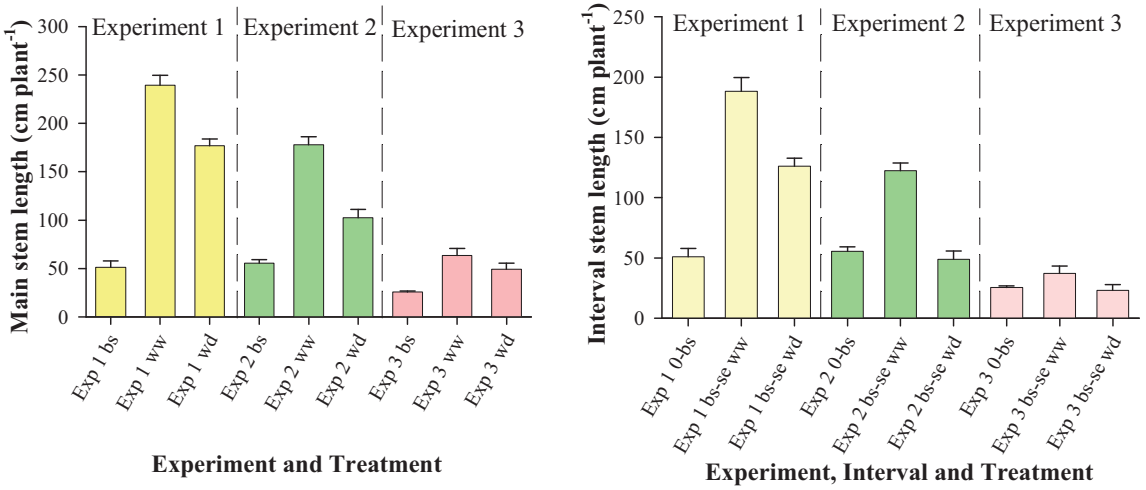

Fig. 13: Mean main stem length and mean interval main stem length before stress (bs), as well as for the well-watered (ww) and water deficit (wd) treatments at se in experiments 1 to 3

The main stem length in the intervals under ww conditions was, on average, 188, 122 and 37 cm in Exp 1, Exp 2 and Exp 3, respectively, which clearly displays the variability of results in the three experiments (Fig. 13). Under wd conditions, there was clear reduction of stem

length, namely 126, 49 and 23 cm in Exp 1, Exp 2 and Exp 3, respectively (Fig. 13). This translates to a 33, 60 and 38 % reduction in the respective experiments. With that the highest relative reduction occurred in Exp 2. The interval response of stem length varied greatly among genotypes (Table 13), particularly in Exp 2, where minimum stem length reduction as low as 7 % and as high as 93/94 % were recorded. In the other two experiments the response was more uniform, with Exp 1 showing a reduction between 27 and 34 %, while it was 22 to to 58 % in Exp 3. This once again highlights the situation of Exp 2, where the more frequent occurrence of pests and the thus necessitated more frequent application of pesticides might possibly have also played an important role in the responses of the genotypes to wd stress.

In comparison with interval DM, interval stem length was less affected by wd in Exp 1, similarly affected in Exp 2 and slightly more affected in Exp 3. On the other hand, stem length was more robust compared to leaf area (LA) in Exp 1, more negatively affected in Exp 2 and less affected in Exp 3.

	Exp 1: Interval stem length (cm)		**Exp 2:** Interval stem length (cm)		**Exp 3:** Interval stem length (cm)	
Genotype	**bs-se (ww)**	**bs-se (wd)**	**bs-se (ww)**	**bs-se (wd)**	**ww**	**wd**
Ex Ukwala	188.3 **b**	121.0 **b**	162.9 **c**	116.6 **d**	**-**	**-**
UCR 328	180.2 **b**	114.9 **b**	113.2 **abc**	8.2 **a**	7,1 **a**	3,0 **a**
UCR 1340	286.0 **c**	189.3 **c**	160.3 **c**	22.8 **ab**	22,1 **c**	11,0 **b**
IT 18	161.1 **ab**	118.4 **b**	126.3 **bc**	8.0 **a**	23,5 **c**	12,1 **b**
UCR 386	186.5 **b**	125.5 **b**	73.3 **a**	34.5 **ab**	18,2 **bc**	11,3 **b**
Lagreen	128.0 **a**	86.7 **a**	161.3 **c**	64.2 **bc**	111,0 **e**	86,8 **d**
Vita 7	-	-	117.6 **abc**	69.1 **bc**	10,6 **ab**	5,8 **ab**
TVu 12348	-	-	97.7 **ab**	91.2 **cd**	**-**	**-**
IFH 27-8	-	-	87.7 **ab**	25.4 **ab**	67,9 **d**	32,8 **c**
Mean	**188,3**	**126,0**	**122,3**	**48,9**	**37,2**	**23,2**

Table 13: Interval stem length [means ± standard error, N = 4 (experiment 1), N = 6 (experiment 2) or N = 5 (experiment 3)] as affected by treatment (ww and wd) in experiment 1 and 2. The same letters signify lack of difference in the appropriate experiment and column ($P < 0.05$).

4.4.3.2. Main stem mass to length ratio (SMLR)

The main stem mass to length ratio (SMLR) is the amount of main stem dry matter (DM) that is produced per unit main stem length (cm). In Exp 1 there was variation among genotypes for SMLR (Table 14). In Exp 2 all genotypes had similar SMLR before stress, but variation was found under ww (se) and wd conditions. No particular treatment or sampling seems to have a

higher or lower SMLR in Exp 1 (Fig. 14). The magnitude of SMLR seems to be dependent on genotype. In Exp 1 Ex Ukwala and Lagreen had the lowest SMLR and UCR 328 the highest in all three categories [bs, ww (se) and wd (se)]. Moreover, the ranking among genotypes was similar in these categories. Lagreen and Ex Ukwala in Exp 2 had the lowest and UCR 328 the highest SMLR in the ww treatment.

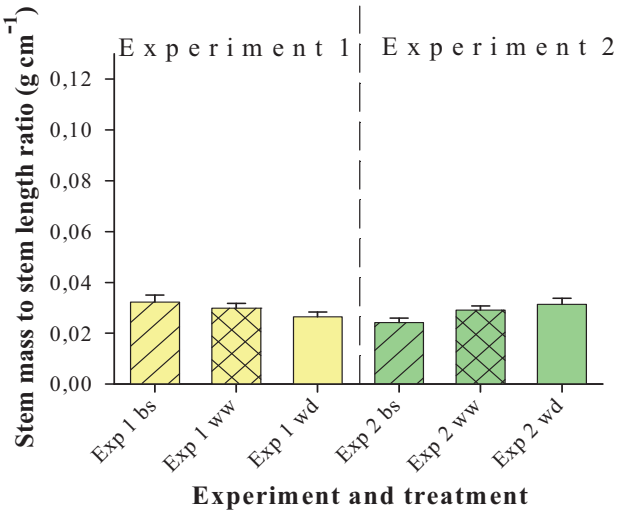

Fig. 14: Mean main stem length to stem mass ratio (SMLR) over all genotypes before stress (bs), as well as for the well-watered (ww) and water deficit (wd) treatments

Drought stress reduced SMLR of five genotypes in Exp 1, with only UCR 328 showing a slight increase (1%), compared with the ww (se). In terms of ranking SMLR under ww (se) and wd conditions in Exp 2 was comparable to that in Exp 1. Water deficit increased SMLR in four genotypes (10 – 53%) and reduced it in five genotypes (3 – 33%). UCR 328 again had an increase of SMLR (47%) under wd stress.

	Experiment 1: SMLR (g cm^{-1})			**Experiment 2:** SMLR (g cm^{-1})		
	ww (bs)	**ww (se)**	**wd (se)**	**ww (bs)**	**ww (se)**	**wd (se)**
Ex Ukwala	0,0206 **a**	0,0209 **a**	0,0174 **a**	0,0162 **ab**	0,0176 **a**	0,0170 **ab**
UCR 328	0,0543 **c**	0,0404 **c**	0,0407 **d**	0,0428 **e**	0,0378 **b**	0,0556 **e**
UCR 1340	0,0328 **b**	0,0253**ab**	0,0202 **a**	0,0264 **cd**	0,0234 **a**	0,0257 **bc**
IT 18	0,0341 **b**	0,0269 **b**	0,0256 **b**	0,0203 **bc**	0,0364 **b**	0,0333 **cd**
UCR 386	0,0371 **b**	0,0441 **c**	0,0342 **c**	0,0316 **d**	0,0415 **b**	0,0359 **cd**
Lagreen	0,0145 **a**	0,0212 **ab**	0,0211 **a**	0,0094 **a**	0,0156 **a**	0,0105 **a**
Vita 7	-	-	-	0,0246 **bcd**	0,0260 **a**	0,0234 **abc**
TVu 12348	-	-	-	0,0247 **bcd**	0,0236 **a**	0,0361 **cd**
IFH 27-8	-	-	-	0,0216 **bcd**	0,0403 **b**	0,0455 **de**
Mean	**0,0322**	**0,0298**	**0,0265**	**0,0242**	**0,0291**	**0,0314**

Table 14: Stem mass to stem length ratio (SMLR) under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and 2 (N = 6). The same letters signify lack of difference in the appropriate experiment and column ($P \leq 0,05$). bs: before stress; se: stress end (maximum wd stress)

4.4.4. Shoot Biomass (DM)

Shoot biomass (DM) (Table 15) varied among genotypes in all experiments at the different sampling dates and treatments. From the harvest before stress (bs) to the ww (se) sampling DM increased more than elevenfold in Exp 1, threefold in Exp 2 and Exp 3. DM in Exp 2 and Exp 3 was much lower than in Exp 1 at corresponding sampling dates. Ex Ukwala and IT 18 which had the highest DM bs had the lowest DM under ww (se) conditions. In Exp 2, IT 18 accumulated the highest DM (13,4 g plant^{-1}) as opposed to Lagreen with the lowest DM (8,3 g plant^{-1}). The latter genotype had produced the least DM at the first harvest (bs). In Exp 3, UCR 328, IT 18 and UCR 386 had the lowest DM, while Lagreen had the highest under ww conditions. These results point to the fact that UCR 328 and IT 18 were low DM genotypes under ww conditions.

	Experiment 1: Biomass (g)			**Experiment 2:** Biomass (g)		
	ww (bs)	**ww (se)**	**wd (se)**	**ww (bs)**	**ww (se)**	**wd (se)**
Ex Ukwala	4,46 **b**	37,76 **a**	17,72 **c**	4,23 **b**	10,52 **ab**	8,58 **d**
UCR 328	3,55 **a**	48,71 **b**	16,72 **bc**	4,66 **b**	11,63 **ab**	4,79 **abc**
UCR 1340	3,25 **a**	47,12 **b**	15,42 **a**	2,24 **a**	9,56 **ab**	2,68 **a**
IT 18	4,56 **b**	39,12 **a**	16,42 **ab**	3,31 **ab**	13,42 **b**	2,99 **ab**
UCR 386	3,63 **a**	44,94 **b**	15,36 **a**	3,16 **ab**	9,40 **ab**	4,83 **abc**
Lagreen	3,87 **ab**	49,55 **b**	17,01 **bc**	1,43 **a**	8,34 **a**	3,31 **ab**
Vita 7	-	-	-	3,05 **ab**	9,90 **ab**	5,60 **bc**
TVu 12348	-	-	-	3,02 **ab**	8,10 **a**	8,97 **d**
IFH 27-8	-	-	-	3,00 **ab**	10,65 **ab**	6,89 **cd**
Mean	**3,89**	**44,54**	**16,44**	**3,12**	**10,17**	**5,40**

Table 15: Shoot biomass (DM) [mean, N = 4 (experiment 1) or N = 6 (experiment 2)] as affected by treatment (ww and wd) in experiment 1 and 2. The same letters signify similarity in the appropriate experiment and column ($P \leq 0,05$). bs: before stress; se: stress end (maximum wd stress)

DM was reduced under stress in all genotypes in all experiments (Table 15). In Exp 1, Ex Ukwala produced the highest DM and also experienced the least relative reduction (53%) of DM compared with the ww (se) treatment. On the other hand, the other genotypes had a 58 – 67% DM decline. In Exp 2, DM under drought went down by 10% (TVu 12348) to 75% (IT 18). The results obtained from the wd stress treatment in Exp 2 confirmed those obtained in Exp 1 that Ex Ukwala is one of those genotypes with the least reduction (18%) of DM.

4.4.4.1. DM accumulation during stress intervals

Under ww conditions mean DM accumulated was 3,89 , 32,82 and 93,06 g plant^{-1} in the intervals planting (0) to before stress (bs), 0-bs, before stress (bs) to stress end (se), bs-se and se to maturity (mat), se-mat, respectively, in Exp 1 (Table 16A). While the biomass

accumulated in Exp 2 (Table 16A) and Exp 3 (Table 16A) in the 0-bs interval was slightly smaller than that in Exp 1, it was manifestly smaller in the later intervals of both experiments. In Exp 1 and Exp 2, each interval contributed a mean of 3 % (0-bs), 25 % (bs-se) and 72 % (se-mat) to the total biomass up to maturity (mat) in Exp 1, while the mean contribution was 12 % (0-bs), 26 % (bs –se) and 62 % (se-mat) in Exp 2. In all genotypes in Exp 1 the 0-bs interval had only a low contribution (2 – 4 %) and the interval bs-se contributed 24 – 35 %, except Ex Ukwala (14 %) with a low contribution in this interval. In the next interval (se-mat) Ex Ukwala had the most biomass accumulation where it accumulated 84 % of total shoot biomass and the other genotypes accumulated between 62 and 73 % in this interval alone. In Exp 2 there was a larger variation in the relative contributions of the intervals. The interval 0-bs contributed 5 – 21 %, bs-se 15 – 43 % and se-mat 40 – 78 %, with Ex Ukwala (73 %) and Vita 7 (78 %) having the highest contribution of the interval se-mat to total DM accumulation up to maturity.

	A well-watered (ww) treatment							
	Experiment 1			Experiment 2			Experiment 3	
Genotype	**0-bs**	**bs-se**	**se-mat**	**0-bs**	**bs-se**	**se-mat**	**0-bs**	**bs-se**
Ex U	4,46 b	25,80 a	155,28 c	4,23 b	6,30 ab	29,00 d	-	-
U328	3,55 a	37,17 b	66,39 a	4,66 b	6,97 ab	10,27 ab	1,94 ab	3,77 a
U1340	3,25 a	35,87 b	84,70 ab	2,24 a	7,32 ab	15,98 bc	2,20 b	5,73 d
IT18	4,56 b	26,56 a	73,88 a	3,31 ab	10,11 b	9,93 ab	2,15 b	3,84 e
U386	3,63 a	33,32 b	99,91 b	3,16 ab	6,23 ab	15,74 bc	1,65 a	4,10 f
Lag	3,87 ab	38,18 b	78,23 ab	1,43 a	6,91 ab	17,97 c	2,99 d	6,09 g
Vita 7	-	-	-	3,05 ab	6,86 ab	35,92 e	2,58 c	3,89 b
TVu	-	-	-	3,02 ab	5,08 a	8,90 ab	-	-
IFH	-	-	-	3,00 ab	7,65 ab	7,12 a	1,90 ab	5,75 c
Mean	**3,89**	**32,82**	**93,06**	**3,12**	**7,05**	**16,76**	**2,20**	**4,74**

	B water deficit (wd) treatment							
	Experiment 1			Experiment 2			Experiment 3	
Genotype	**0-bs**	**bs-se**	**se-mat**	**0-bs**	**bs-se**	**se-mat**	**0-bs**	**bs-se**
Ex U	4,46 **b**	13,25 **b**	113,95 **d**	4,23 **b**	4,36 **cd**	21,77 **b**	-	-
U328	3,55 **a**	13,18 **b**	78,97 **b**	4,66 **b**	1,50 **b**	9,78 **a**	1,94 **ab**	2,70 **a**
U1340	3,25 **a**	12,17 **ab**	78,56 **b**	2,24 **a**	0,52 **a**	5,42 **a**	2,20 **b**	2,95 **d**
IT18	4,56 **b**	11,86 **ab**	58,62 **a**	3,31 **ab**	1,26 **b**	8,68 **a**	2,15 **b**	3,21 **e**
U386	3,63 **a**	11,73 **a**	134,95 **e**	3,16 **ab**	2,70 **abc**	19,85 **b**	1,65 **a**	3,01 **f**
Lag	3,87 **ab**	13,14 **b**	94,32 **c**	1,43 **a**	2,01 **abc**	21,01 **b**	2,99 **d**	4,73 **g**
Vita 7	-	-	-	3,05 **ab**	2,64 **abc**	34,25 **c**	2,58 **c**	2,41 **b**
TVu	-	-	-	3,02 **ab**	5,95 **d**	6,52 **c**	-	-
IFH	-	-	-	3,00 **ab**	3,97 **bcd**	8,02 **a**	1,90 **ab**	3,41 **c**
Mean	**3,89**	**12,56**	**93,23**	**3,12**	**2,77**	**15,03**	**2,20**	**3,20**

Table 16: Shoot biomass, DM (g plant^{-1}) in the intervals planting to before stress, also flowering onset (0-bs), before stress to stress end (bs – se) and from stress end to maturity (se – mat) in Exp 1 (N = 4), Exp 2 (N = 6) and Exp 3 (N = 5) in the well-watered (ww), ***A*** and water deficit (wd), ***B*** treatments. Same letters in a column show lack of significance (P ≤ 0,05) among genotypes according to Duncan's Multiple Range Test.

Under wd conditions mean DM accumulated in the intervals amounted to 3,89 g plant^{-1} (0-bs), 12,56 g (bs-se) and 93,25 g (se-mat) in Exp 1, 3,12 g (0-bs), 2,77 g (bs-se) and 15,03 g (se-mat) in Exp 2 and 2,20 g (0-bs) and 3,20 g (bs-se) in Exp 3 (Table 16B). In the first two experiments, this was a mean relative contribution to biomass of 4 %, 12 % and 84 % in the 0-bs, bs-se and se-mat intervals, respectively in Exp 1; while it was 15 % (0-bs), 13 % (bs-se) and 72 % (se-mat) in Exp 2. As to be expected, the relative contribution of the 0-bs interval was unaffected under wd stress, but was reduced, on average, by around 50 % in the bs-se interval in both Exp 1 and Exp 2; thereby increasing the mean relative contribution of the following interval by about 10 percentage points in both experiments. Most genotypes reacted to wd stress by increasing their DM accumulation after relief of stress, except Ex Ukwala which had a minimal relative increase (compared to ww conditions) of 3 % (from 84 % in the se-mat interval under ww conditions to 87 % under wd conditions in Exp 1, and it even reduced by 1 percentage point in Exp 2). This shows that most genotypes tend to have a compensatory biomass accumulation after their release from stress.

4.4.4.2. Biomass stress indices

A water deficit stress susceptibility index (SSI) and water deficit stress intensity index (SII), based on shoot biomass (DM) at final maturity, were determined for both Exp 1 and Exp 2. Water deficit stress susceptibility index (SSI) and water deficit stress intensity index (SII) (Fischer and Maurer, 1978) were determined as follows:

$SII = 1 - (X_s/X_{ns})$, where X_s is mean experiment DM of all genotypes grown under drought stress and X_{ns} is mean experiment DM of all genotypes grown under non-stress conditions.

$SSI = [1 - (Y_s/Y_{ns})]/SII$, where Y_s is genotypic performance under stress conditions and Y_{ns} is genotypic performance under non-stress conditions.

SII is a measure of the severity of water deficit stress based on DM, which permits values to be compared among experiments and environments.

Stress susceptibility index (SSI) based on DM (SSI_{DM}) displayed two distinct groups in Exp 1 (Fig. 17), with values varying from 0,408 to 1,801. Lagreen had the lowest value although this was not distinguishable from those of UCR 328, UCR 386 and UCR 1340. IT 18 and Ex Ukwala had the highest values. A water deficit stress intensity index (SII) based on DM (SII_{DM}) was determined. This was 0,155 for the DM in Exp 1.

In Exp 2 there was a larger variation for SSI_{DM} among genotypes which ranged from 0,192 to 2,844 (Fig. 17). The ranking for SSI_{DM} differed from that in Exp 1. However, Lagreen had the lowest SSI_{DM} and UCR 1340 was among those with the highest SSI_{DM} values. The SII_{DM} at 0,241 was well above that in Exp 1, indicating a greater stress level in Exp 2.

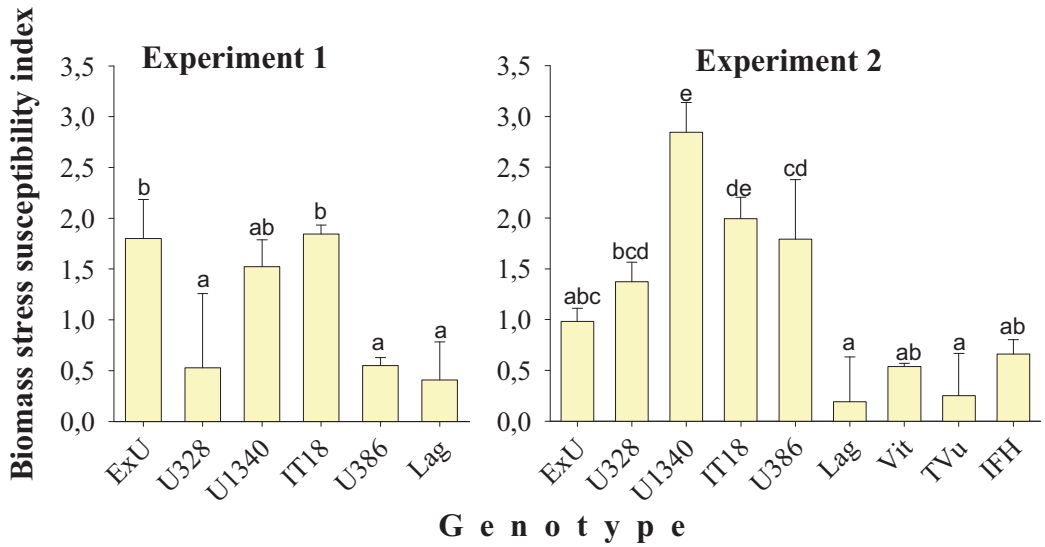

Fig. 15: Water deficit stress susceptibility index (SSI) at maturity for biomass (SSI_{DM}) (± standard error) for experiment 1 and 2. Same letters in an experiment show lack of significance ($P \leq 0,05$) among genotypes according to Duncan's Multiple Range Test.

4.4.5. Leaf area and specific leaf area

4.4.5.1. Leaf area (LA)

Leaf area (LA) development was different among genotypes (Table 17) so that in Exp 1 two distinct groups could be established before stress, but the variation among genotypes was more under ww (se) and wd (se) conditions. LA was generally lower in Exp 2 than in Exp 1 in all three categories, except in the case of UCR 328 before stress. LA before stress was 9 – 18% of LA in the ww (se) treatment. In Exp 2, LA before stress relative to ww (se) was higher than in Exp 1 being 24 – 68% of ww (se). Ranking for LA under ww (se) conditions differed between the two experiments. In Exp 1 LA under water deficit declined in all genotypes by 50 – 66%. Water deficit in Exp 2 reduced LA by 7 – 65%, being lowest in Ex Ukwala. Ex Ukwala had the highest LA under wd stress in both experiments.

In the interval (Table 18), mean LA was 5883, 915 and 615 cm² under ww conditions in Exp 1, Exp 2 and Exp 3, respectively. The values reflect the inconsistency of the results also recorded elsewhere for other traits among these three experiments. Water deficit conditions reduced interval LA by 67 % in Exp 1 and 51 % in Exp 2 and 3. UCR 386 was the most

consistent genotype in the three experiments, being among the genotypes with the highest interval LA under both ww and wd conditions. IT 18 generally tended to have low interval LA. In Exp 1 the reduction ranged between 59 and 72/73 %, 13 and 86 % in Exp 2 and 5 to 73/75 % in Exp

	Experiment 1: Leaf area, LA (cm²)			**Experiment 2:** Leaf area, LA (cm²)		
	ww (bs)	**ww (se)**	**wd (se)**	**ww (bs)**	**ww (se)**	**wd (se)**
Ex Ukwala	1009,83 **b**	6485,13 **b**	3262,28 **c**	794,00 **bc**	1889,25 **b**	1744,80 **d**
UCR 328	726,41 **a**	6263,21 **b**	2675,32 **b**	929,24 **c**	1369,74 **a**	767,29 **ab**
UCR 1340	722,60 **a**	7920,95 **d**	2694,40 **b**	518,79 **ab**	1428,28 **ab**	538,84 **a**
IT 18	996,66 **b**	5404,38 **a**	2215,52 **a**	820,60 **bc**	1497,66 **ab**	529,55 **a**
UCR 386	753,29 **a**	6974,65 **bc**	2906,99 **b**	689,78 **bc**	1534,61 **ab**	1009,87 **ab**
Lagreen	815,36 **ab**	7275,75 **cd**	2881,51 **b**	359,74 **a**	1511,54 **ab**	665,18 **ab**
Vita 7	-	-	-	718,60 **bc**	1943,89 **b**	1104,20 **bc**
TVu 12348	-	-	-	758,15 **bc**	1658,78 **ab**	1539,22 **cd**
IFH 27-8	-	-	-	715,47 **bc**	1705,38 **ab**	749,80 **ab**
Mean	837,36	6720,68	2772,67	700,48	1615,46	960,97

Table 17: Leaf area (LA) [mean, N = 4 (experiment 1) or N = 6 (experiment 2)] as affected by treatment (ww and wd) in experiment 1 and 2. The same letters signify lack of difference in the appropriate experiment and column ($P \leq 0,05$).

3. Interval LA mean reduction (67 %) was close to that of DM (62 %) in Exp 1, 51 % (interval LA) vs 61 % (interval DM) in Exp 2 and 51 % (interval LA) vs 32 % (interval DM) in Exp 3.

	Experiment 1: Interval leaf area (cm²)		**Experiment 2:** Interval leaf area (cm²)		**Experiment 3:** Interval leaf area (cm²)	
Genotype	**ww**	**wd**	**ww**	**wd**	**ww**	**wd**
Ex Ukwala	5475,30 **b**	2252,45 **b**	1095,25 **bc**	950,80 **d**	-	-
UCR 328	5536,80 **b**	1948,91 **b**	440,51 **a**	279,67 **ab**	471,58 **ab**	268,40 **ab**
UCR 1340	7198,35 **d**	1971,80 **b**	909,49 **abc**	123,39 **ab**	841,87 **d**	332,53 **b**
IT 18	4407,73 **a**	1218,87 **a**	677,05 **ab**	336,49 **a**	435,21 **ab**	298,58 **b**
UCR 386	6221,37 **bc**	2153,70 **b**	844,83 **abc**	518,08 **bc**	562,82 **bc**	476,22 **c**
Lagreen	6460,39 **cd**	2066,15 **b**	1151,80 **bc**	361,04 **bc**	927,90 **d**	250,26 **ab**
Vita 7	-	-	1225,30 **c**	427,83 **bc**	333,34 **a**	317,16 **b**
TVu 12348	-	-	900,64 **abc**	781,08 **cd**	-	-
IFH 27-8	-	-	989,91 **bc**	243,46 **ab**	731,68 **cd**	180,18 **a**
Mean	**5883,32**	**1935,31**	**914,97**	**446,87**	**614,91**	**303,33**

Table 18: Interval leaf area (LA_{int}) [means ± standard error, N = 4 (experiment 1), N = 6 (experiment 2) or N = 5 (experiment 3)] as affected by treatment (ww and wd) in experiment 1 and 2. The same letters signify lack of difference in the appropriate experiment and column ($P < 0.05$).

4.4.5.2. Specific leaf area (SLA)

Specific leaf area (SLA) (Table 19) showed variation among genotypes in Exp 1 at all sampling dates and treatments. In some cases SLA under wd was highest. Drought stress

increased SLA, except in UCR 1340 (6% reduction), by up to 37% compared with the ww (se) treatment. Ex Ukwala had the highest SLA under both treatments. In Exp 2 variation was found before stress and in the ww (se) treatment, but not under wd stress. Like in Exp 1, SLA was not higher in any particular treatment or sampling date. However, there was a slight tendency for SLA under drought to be higher in some genotypes in both experiments. Water deficit influenced SLA by increasing it by 1 – 93%, except in IFH 27-8 where there was a 20% reduction of SLA.

	Experiment 1: Specific leaf area ($cm^2\ g^{-1}$)			**Experiment 2:** Specific leaf area ($cm^2\ g^{-1}$)		
	ww (bs)	**ww (se)**	**wd (se)**	**ww (bs)**	**ww (se)**	**wd (se)**
Ex Ukwala	367,80 **b**	355,35 **d**	416,48 **d**	378,09 **abc**	395,40 **cd**	460,44 **a**
UCR 328	291,27 **a**	241,50 **a**	331,97 **bc**	328,58 **a**	249,51 **a**	364,96 **a**
UCR 1340	328,24 **ab**	334,82 **d**	315,93 **ab**	348,52 **ab**	276,86 **ab**	385,92 **a**
IT 18	348,16 **ab**	274,43 **c**	293,49 **a**	485,98 **cd**	276,91 **ab**	535,79 **a**
UCR 386	298,56 **a**	303,07 **b**	343,96 **c**	353,75 **ab**	302,29 **ab**	413,22 **a**
Lagreen	373,97 **b**	291,23 **bc**	332,99 **bc**	592,60 **d**	354,32 **bc**	379,02 **a**
Vita 7	-	-	-	443,28 **abc**	385,88 **cd**	430,32 **a**
TVu 12348	-	-	-	396,77 **abc**	345,68 **bc**	348,34 **a**
IFH 27-8	-	-	-	456,03 **bc**	438,96 **d**	349,62 **a**
Mean	334,67	300,07	339,14	420,40	336,20	407,51

Table 19: Specific leaf area, SLA ($cm^2\ g^{-1}$) before stress and at stress end (maximum stress) for both Experiment 1 and 2. The same letters signify lack of difference between genotypes in the appropriate experiment and column ($P \leq 0,05$).

4.4.6. Stem mass ratio and leaf mass ratio

4.4.6.1. Stem mass ratio (SMR)

Stem mass ratio (SMR) (Table 20) represents the ratio of stem DM to shoot biomass. In Exp 1 SMR was lowest under ww (se) conditions, and in some cases highest in the wd treatment (UCR 328 and UCR 386) and in the remaining four genotypes highest before stress. There was variation for SMR in both experiments. Water deficit led to an increase in SMR in both experiments. In Exp 2 UCR 328, IT 18 and IFH 27-8 generally had the highest SMR in all categories, confirming the results obtained in Exp 1.

	Experiment 1: Stem mass ratio			**Experiment 2:** Stem mass ratio		
	ww (bs)	**ww (se)**	**wd (se)**	**ww (bs)**	**ww (se)**	**wd (se)**
Ex Ukwala	0,342 **c**	0,143 **bc**	0,192 **a**	0,453 **c**	0,468 **abc**	0,481 **ab**
UCR 328	0,278 **a**	0,165 **c**	0,324 **c**	0,371 **c**	0,498 **bcd**	0,557 **b**
UCR 1340	0,315 **bc**	0,169 **c**	0,289 **bc**	0,325 **a**	0,459 **abc**	0,471 **ab**
IT 18	0,307 **ab**	0,139 **b**	0,254 **b**	0,421 **c**	0,512 **cd**	0,542 **ab**
UCR 386	0,302 **ab**	0,210 **d**	0,342 **c**	0,363 **ab**	0,448 **abc**	0,484 **ab**
Lagreen	0,417 **d**	0,104 **a**	0,245 **b**	0,501 **d**	0,428 **ab**	0,436 **a**
Vita 7	-	-	-	0,458 **c**	0,461 **abc**	0,532 **ab**
TVu 12348	-	-	-	0,361 **ab**	0,396 **a**	0,505 **ab**
IFH 27-8	-	-	-	0,419 **c**	0,556 **d**	0,565 **b**
Mean	**0,327**	**0,155**	**0,274**	**0,408**	**0,469**	**0,508**

Table 20: Stem mass ratio (SMR) under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and 2 (N = 6). The same letters signify lack of difference in the appropriate experiment and column ($P \leq 0,05$). bs: before stress; se: stress end (maximum wd stress)

4.4.6.2. Leaf mass ratio (LMR)

Leaf mass ratio (LMR) (Table A11) is the ratio of leaf DM to shoot biomass. In Exp 1 and 2 LMR varied among genotypes. Under ww (se) conditions UCR 386 had the highest and IT 18 the lowest LMR and this trait under wd conditions was highest in UCR 386, and lowest in UCR 1340 and Ex Ukwala. LMR declined under wd in Exp 1 in three genotypes (2 – 10%) and increased in the other three (1 – 11%). In Exp 2 TVU 12348, UCR 1340, UCR 386 and Lagreen had the highest LMR under ww (se) conditions, while IFH 27-8 had the lowest. Under wd stress in Exp 2 Lagreen, UCR 1340 and UCR 386 had the highest LMR and again IFH 27-8 the lowest. In two genotypes under wd stress LMR increased (4 – 6%), but it declined (2 – 19%) in all other genotypes. It looks like UCR 1340 and UCR 386 generally have high LMR in both treatments.

4.4.6.3. Leaf shedding

Leaf shedding in all three experiments was scored according to the scheme shown in Table 21 at the maximum stress level (stress end, se) in each experiment.

There was leaf shedding in the ww treatment in most genotypes (Table 22) in all experiments. The genotypes, which did not shed some leaves under ww conditions, were UCR 386 (Exp 1 and 3), TVu 12348 (Exp 2) and UCR 1340 (Exp 3). Ex Ukwala had the highest LSS in both Exp 1 and Exp 2. In the third experiment, IT 18 and Vita 7 had the highest LSS.

Score	Description
0	no leaves shed
1	both primary leaves shed
2	primary leaves and 1 trifoliate leaf shed
3	primary leaves and 2 trifoliate leaves shed
4	primary leaves and 3 trifoliate leaves shed
5	primary leaves and 4 trifoliate leaves shed
6	primary leaves and 5 trifoliate leaves shed

Table 21: Scheme used for leaf shedding score (LSS) in all experiments for the well-watered (ww) and water deficit (wd) treatments

Under wd conditions, for most genotypes LSS was higher than under ww conditions in all experiments (Table 22), except UCR 328 which always had a one-point lower LSS in the wd treatment than in the ww treatment in all experiments. Those genotypes with low LSS in the ww treatment also displayed lower LSS under wd conditions. In this regard, the most conspicuous were UCR 328, UCR 386, TVu 12348 and IFH 27-8. UCR 328 was the most consistent genotype in all three experiments under ww (LSS = 1) and wd (LSS = 0) conditions. The ranking for LSS under wd was similar, with minor deviations, in all three experiments. Furthermore, ranking under wd conditions was also similar to that under ww conditions.

	Experiment 1				**Experiment 2**				**Experiment 3**			
	well watered		**water deficit**		**well watered**		**water deficit**		**well watered**		**water deficit**	
	LSS	**Nodes**	**LSS**	**Nodes**	**LSS**	**Nodes**	**LSS**	**Nodes**	**LSS**	**Nodes**	**LSS**	**Nodes**
Ex U	4	18	6	13	3	18	6	13	-	-	-	-
U328	1	18	0	13	1	11	0	8	1	11	0	8
U1340	2	17	4	14	2	13	4	7	0	10	5	9
IT18	2	15	4	13	2	11	4	7	3	11	5	9
U386	0	14	2	12	1	9	2	8	0	10	3	7
Lag	2	13	4	12	2	13	4	8	2	12	5	10
Vita7	-	-	-	-	2	18	4	14	3	13	6	11
TVu	-	-	-	-	0	14	0	12	-	-	-	-
IFH	-	-	-	-	1	15	2	9	1	12	3	10
Mean	**2**	**16**	**3**	**13**	**2**	**14**	**3**	**10**	**2**	**11**	**4**	**9**

Table 22: Leaf shedding score (LSS) under well-watered (ww) and water deficit (wd) conditions and the corresponding total number of leaf nodes (Nodes) at the end of stress in experiments 1 to 3

4.5. Electrolyte leakage and leaf temperature

4.5.1. Cell membrane stability (CMS)

Electrolyte leakage was determined in Exp 2 and Exp 3 before stress (bs) and at stress end (se). Cell membrane stability (CMS) under stress was used to evaluate electrolyte leakage. CMS of the wd treatment was calculated according to the formular: CMS (%) = [1-(EC_{1wd}/EC_{2wd})]/[1-(EC_{1ww}/EC_{2ww})]*100, where EC_1 is the first electrical conductivity determined twenty-four hours before autoclaving and EC_2 the second electrical conductivity determined after autoclaving and the subscripts wd and ww stand for water deficit and well-watered treatment, respectively (refer to Materials and Methods for more details).

Cell membrane stability (CMS) of the wd treatment compared to the ww treatment was determined from the electrolyte leakage data in Exp 2 and Exp 3. Mean CMS (Table 23) in Exp 2 (92 %) was lower than in Exp 3 (94 %). Variation for CMS existed among genotypes (Table 23), whereby CMS varied from 88 % (Ex Ukwala) to 95 % (IFH 27-8 and UCR 328) in Exp 2 and from 90 % (IT 18) to 97 % (IFH 27-8) in Exp 3. In all genotypes, CMS in Exp 2 was lower than that in Exp 3. For the genotypes common to both experiments the ranking was generally similar, with UCR 386 and Vita 7 altering their from high (UCR 386) and low (Vita 7) in Exp 2 to intermediate (UCR 386) and high (Vita 7) in Exp 3.

Genotype	Exp 2 CMS (%), wd	Exp 3 CMS (%), wd
Ex Ukwala	87,59 ± 1,16 a	-
UCR 328	95,10 ± 0,11 d	96,31 ± 0,39 de
UCR 1340	91,87 ± 0,59 c	94,96 ± 0,16 cd
IT 18	89,25 ± 0,28 b	89,88 ± 0,71 a
UCR 386	92,56 ± 0,39 c	93,71 ± 0,38 bc
Lagreen	91,67 ± 0,50 c	93,36 ± 0,61 b
Vita 7	90,99 ± 0,14 c	95,08 ± 0,32 cd
TVu 12348	94,69 ± 0,16 d	-
IFH 27-8	95,08 ± 0,52 d	96,90 ± 0,46 e
Mean	**92,09** ± 0,38	**94,32** ± 0,40

Table 23: Cell membrane stability, CMS (means ± standard error) under water deficit (wd) conditions for experiment 2 and 3. Means followed by the same letter are not significantly different in the appropriate column and experiment ($P \leq 0,05$; Duncan's Multiple Range Test).

According to these results, IT 18 and Lagreen tend to have a low CMS under wd stress and at the other end of the spectrum UCR 328 and IFH 27-8 have tissues which remained relatively stable under wd stress. CMS of UCR 1340 was intermediate in both experiments.

4.5.2. Leaf temperature

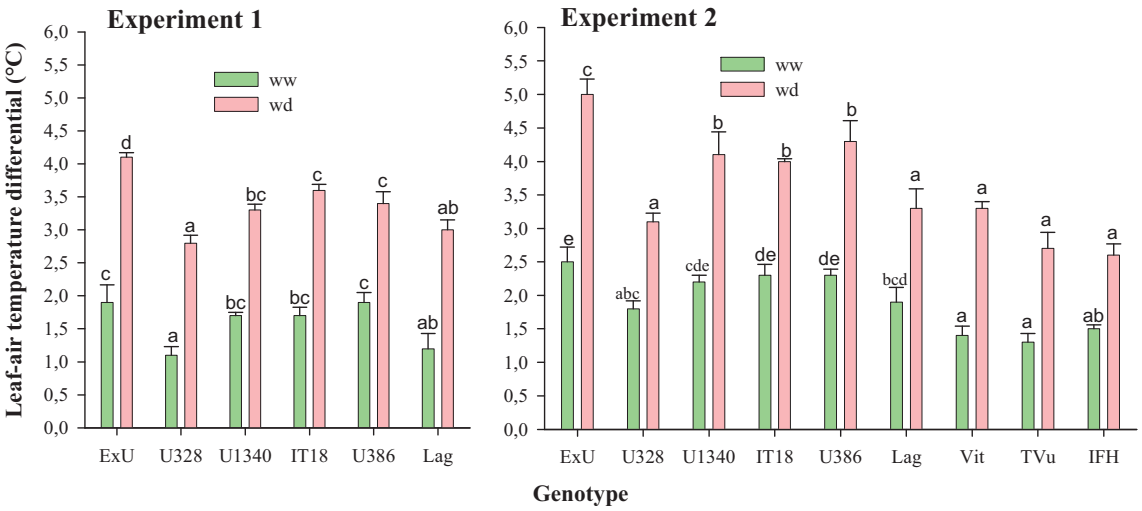

Fig. 16: Leaf-air temperature differential, ΔT, (°C) (means ± standard error) of well-watered (ww) and water deficit (wd) treatments for experiment 1 and 2. The same letters signify lack of difference in the appropriate experiment and column ($P \leq 0,05$). Leaf-air temperature differential: T_{leaf} minus T_{air}

Leaf temperature was determined as a leaf-air temperature differential (hereafter referred to as 'ΔT'), that is leaf temperature (T_{leaf}) subtract air temperature (T_{air}) at stress end (se). There were differences among genotypes, with ΔT ranging from 1,1°C to 1,9°C under ww conditions and the mean was 1,6°C in Exp 1 (Fig. 15). In Exp 2, ΔT was higher than in Exp 1 under ww conditions for the six genotypes common to both experiments (Fig. 15), which was also reflected in the higher mean ΔT for all nine genotypes (1,9°C).

Water deficit (wd) induced a rise in ΔT in both experiments (Fig. 15). The ranking of genotypes was similar to that under ww conditions. In Exp 2 in the wd treatment, genotypic ΔT values were also higher than in Exp 1. Again Ex Ukwala (5,0°C) was way above all the other genotypes. The ranking was also close to that under ww conditions in this experiment, with a small distortion from Lagreen. It is interesting to note that Ex Ukwala and Lagreen generally had relatively large standard errors in both treatments in Exp 2.

4.6. Yield and yield components

4.6.1. Number of pods and seeds

Only Exp 1 and Exp 2 were conducted till the plants were mature. Consequently, yield results of only these two experiments are presented here.

4.6.1.1. Number of pods

	Exp 1: Number of pods		**Exp 2:** Number of pods	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	3 ± 1 **a**	1 ± 0 **a**	-	-
UCR 328	19 ± 2 **b**	21 ± 1 **b**	6 ± 0 **c**	5 ± 1 **c**
UCR 1340	31 ± 1 **c**	27 ± 3 **bc**	7 ± 1 **cd**	2 ± 1 **b**
IT 18	31 ± 2 **c**	22 ± 1 **b**	8 ± 1 **cd**	3 ± 0 **bc**
UCR 386	38 ± 1 **d**	31 ± 5 **c**	8 ± 1 **d**	4 ± 1 **c**
Lagreen	35 ± 4 **cd**	28 ± 1 **bc**	3 ± 1 **b**	3 ± 0 **bc**
Vita 7	**-**	**-**	-	-
TVu 12348	**-**	**-**	4 ± 1 **b**	3 ± 0 **b**
IFH 27-8	**-**	**-**	7 ± 1 **cd**	4 ± 1 **cd**
Mean	**26 ± 3**	**22 ± 2**	**6 ± 0**	**3 ± 0**

Table 24: Number of pods (means ± standard error) under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and experiment 2 (N = 6). The same letters signify lack of difference in the respective experiment and column ($P \leq 0,05$).

In the ww treatment the pod number averaged over all genotypes was 26 and 6 pods plant^{-1} (Table 24) in Exp 1 and Exp 2, respectively, showing the much lower level of pod production in Exp 2. There was variation among genotypes for pod number in the ww treatment in both experiments (Table 24). The lowest number of pods plant^{-1} in Exp 1 was 3 (Ex Ukwala) as oppossed to 38 pods plant^{-1} realised by UCR 386. In Exp 2 Ex Ukwala and Vita 7 did not flower. Of those that flowered, pod number plant^{-1} varied from 3 (Lagreen) to 8 (IT 18 and UCR 386). This was very low, in particular compared to Exp 1.

Water deficit at the onset of flowering gave rise to a reduction of number of pods plant^{-1} in both experiments, on average by 15 % (Exp 1) and 40 % (Exp 2). The mean in the wd treatment was 22 and 3 pods plant^{-1} in Exp 1 and Exp 2 (Table 24), respectively, again exhibiting a huge difference in pod production between the two experiments. There was genotypic variation for pods plant^{-1} in the wd treatment in both experiments. While only UCR 328 showed a constant number of pods plant^{-1} (negligible increase in the wd treatment in Exp 1) in both experiments, Lagreen had a constant number of pods plant^{-1} in Exp 2. In Exp 1 the range of number of pods plant^{-1} was 1 (Ex Ukwala) to 31 (UCR 386) and in Exp 2 it was 2 (UCR 1340) to 5 (UCR 328). The reduction of pods plant^{-1} was 13 % (UCR 1340) to 67 %

(Ex Ukwala) in Exp 1, where only UCR 328 had an increase 0f 10 %. In Exp 2 the reduction was in the wd treatment was 0 % (Lagreen) to 71 % (UCR 1340).

4.6.1.2. Number of seeds

	Experiment 1: Number of seeds		**Experiment 2:** Number of seeds	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	37 ± 11 **a**	5 ± 3 **a**	-	-
UCR 328	220 ± 14 **b**	238 ± 4 **b**	60 ± 3 **cd**	35 ± 6 **bcd**
UCR 1340	349 ± 29 **cd**	347 ± 56 **c**	74 ± 8 **cd**	20 ± 4 **b**
IT 18	422 ± 8 **e**	286 ± 14 **bc**	98 ± 8 **e**	28 ± 4 **bc**
UCR 386	393 ± 6 **de**	315 ± 34 **bc**	80 ± 12 **de**	30 ± 10 **bc**
Lagreen	296 ± 31 **c**	256 ± 5 **b**	58 ± 5 **bc**	49 ± 4 **d**
Vita 7	-	-	-	-
TVu 12348	-	-	38 ± 7 **b**	39 ± 4 **cd**
IFH 27-8	-	-	54 ± 7 **bc**	33 ± 4 **bc**
Mean	**286 ± 28**	**241 ± 25**	**66 ± 4**	**33 ± 2**

Table 25: Number of seeds (means ± standard error) under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and experiment 2 (N = 6). The same letters signify lack of difference in the appropriate experiment and column ($P \leq 0,05$).

On average, the number of seeds plant^{-1} in the ww treatment (Table 25) was 286 and 66 in Exp 1 and Exp 2, respectively, reflecting the stark difference in the two experiments also exhibited by number of pods plant^{-1}. In Exp 1, number of seeds plant^{-1} varied among genotypes (Table 25), with Ex Ukwala having very low (37) and IT 18 the highest (422) number of seeds plant^{-1}. The genotypic ranking for number of seeds generally reflected that of number of pods, with minor changes, especially IT 18 had the highest number of seeds plant^{-1} although it was ranked only intermediate for number of pods. In Exp 2, number of seeds plant^{-1} ranged between 0 (Ex Ukwala) and 98 (IT 18). The genotypic ranking was similar to that in Exp 1 when considering only the six genotypes common to both experiments. Of the three additional genotypes, Vita 7 did not flower, TVu 12348 ranked low and IFH 27-8 was intermediate. This ranking also reflected that of number of pods.

Water deficit (wd) gave rise to a reduction of number of seeds plant^{-1}, on average by 16 % (Exp 1) and 49 % (Exp 2), values close to those for the reduction of number of pods. There was genotypic variation for number of seeds plant^{-1} in both experiments. The values in Exp 1 extended from 5 (Ex Ukwala) to 347 (UCR 1340). Ex Ukwala was a clear outlier, just as in the ww treatment, which became clearer in Exp 2, where it did not flower (along with Vita 7). In Exp 2, number of seeds plant^{-1} ranged from 20 (UCR 1340) to 49 (Lagreen), excluding Ex Ukwala and Vita 7 which did not flower in both treatments. The highest reduction was found

in UCR 1340 (73 %) and IT 18 (71 %), while the least reduction was observed in TVu 12348 (3 %) and Lagreen (16 %).

4.6.2. Seed yield

Seed yield plant^{-1} (Table 26) in Exp 1 and 2 in both treatments varied among genotypes. In Exp 1 seed yield varied between 3,8 g plant^{-1} (Ex Ukwala) and 48.6 g plant^{-1} (IT 18) in the control treatment. Ex Ukwala had the lowest yield in both treatments. Although Ex Ukwala and Vita 7 were allowed to grow for six months, a period much longer than for any other genotype in Exp 2, these two genotypes did not flower in Exp 2. Under ww conditions UCR 328 and IT 18 produced the highest seed yield in Exp 2, while TVu 12348 had the lowest seed yield in both treatments. The results in Exp 2 confirmed UCR 328 and IT 18 as having the best seed yield under continuous full irrigation (control).

	Experiment 1: Seed yield (g)		**Experiment 2:** Seed yield (g)	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	3,80 ± 1,01 **a**	0,43 ± 0,28 **a**	-	-
UCR 328	46,98 ± 2,97 **cd**	42,81 ± 1,80 **c**	13,13 ± 0,45 **c**	8,28 ± 0,95 **b**
UCR 1340	39,83 ± 3,01 **bc**	35,58 ± 3,23 **b**	10,08 ± 0,78 **b**	4,10 ± 0,43 **a**
IT 18	48,58 ± 1,65 **d**	33,38 ± 0,95 **b**	13,15 ± 1,22 **c**	5,36 ± 0,50 **a**
UCR 386	37,64 ± 1,30 **b**	31,98 ± 3,73 **b**	8,92 ± 1,07 **b**	4,33 ± 0,78 **a**
Lagreen	40,04 ± 4,42 **bc**	34,04 ± 0,79 **b**	8,67 ± 0,85 **b**	6,75 ± 0,59 **b**
Vita 7	-	-	-	-
TVu 12348	-	-	5,71 ± 0,51 **a**	5,14 ± 0,31 **a**
IFH 27-8	-	-	9,44 ± 0,84 **b**	8,13 ± 0,58 **b**
Mean	**36,15** ± 3,27	**29,70** ± 2,93	**9,87** ± 0,46	**6,01** ± 0,48

Table 26: Seed yield (means ± standard error) under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and experiment 2 (N = 6). The same letters signify lack of difference in the appropriate experiment and column (P ≤ 0,05). bs: before stress; se: stress end (maximum wd stress)

In Exp 1, seed yield varied from 0,4 (Ex Ukwala) to 42,8 g plant^{-1} (UCR 328) under wd stress. The drought treatment in Exp 1 experienced a seed yield reduction relative to the control treatment by a margin of 9 (UCR 328) to 89% (Ex Ukwala). UCR 328 produced the highest yield under wd stress. UCR 328 and IFH 27-8 had the highest seed yield under wd stress. In the two treatments seed yield in Exp 2 was lower than a third of that in Exp 1. UCR 328 is confirmed as producing high seed yield under drought stress. Drought led to a 10 – 59% reduction of seed yield in Exp 2.

4.6.2.1. Seed yield stress index

Similar to biomass, a water deficit stress susceptibility index (SSI) and water deficit stress intensity index (SII), based on dry matter (DM) at final maturity and seed yield, were determined for both Exp 1 and Exp 2.

After the final seed yield was obtained in Exp 1 and Exp 2, the water deficit stress susceptibility index (SSI) and the water deficit stress intensity index (SII) (Fischer and Maurer, 1978) were determined as follows:

$SII = 1 - (X_s/X_{ns})$, where X_s is mean experiment yield of all genotypes grown under drought stress and X_{ns} is mean experiment yield of all genotypes grown under non-stress conditions.

$SSI = [1 - (Y_s/Y_{ns})]/SII$, where Y_s is genotypic performance under stress conditions and Y_{ns} is genotypic performance under non-stress conditions

SII is a measure of the severity of water deficit stress based on yield, which permits values to be compared among experiments and environments.

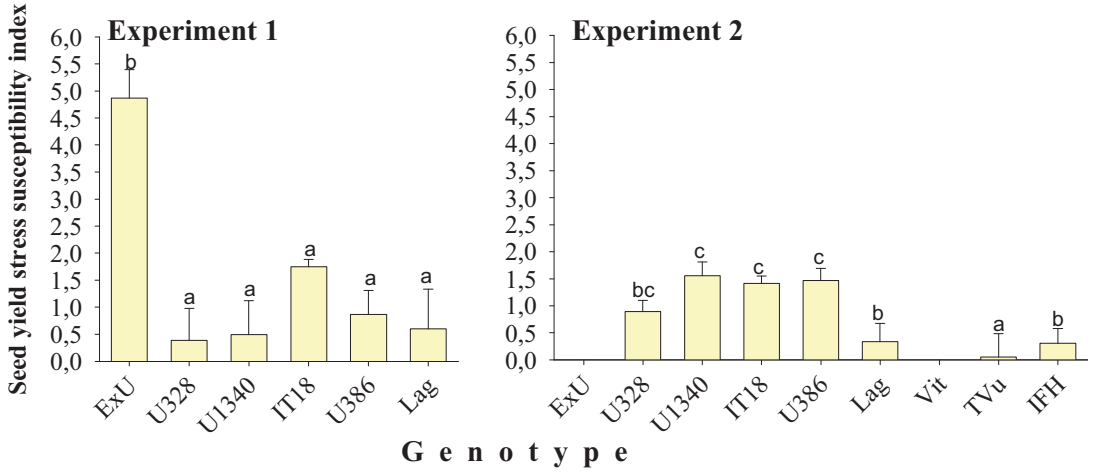

Fig. 17: Water deficit stress susceptibility index (SSI) for seed yield (SSI_{yield}) (means ± standard error) for experiment 1 and experiment 2. The same letters signify lack of difference among genotypes in the respective experiment ($P \leq 0,05$) according to Duncan's Multiple Range Test.

SSI determined on the basis of seed yield (SSI_{yield}) showed that only Ex Ukwala, with its very high SSI_{yield} of 4,867, was distinct from the other five genotypes, which had SSI_{yield} values ranging from 0,386 to 1,746 (Fig. 16). Although SSI_{yield} of UCR 328 was not significantly different from that of the other four genotypes, it was the lowest and this time UCR 1340 (0,493) had a low SSI_{yield}. A calculation of water deficit stress index (SII) based on seed yield (SII_{yield}) in Exp 1 yielded 0,178 – a value higher than that for SII_{DM} (0,155) in this experiment. In Exp 2, Ex Ukwala and Vita 7 were not included in the calculation of SSI_{yield}

since they did not flower. In the five genotypes common to both experiments, Lagreen had the lowest SSI_{yield} (0,339) which was similar to that of UCR 328 (0,896), while the other three genotypes had similar values (1,413 to 1,559) (Fig. 16). The two additional genotypes, i. e. TVu 12348 and IFH 27-8, in Exp 2 had low SSI_{yield} values of 0,052 and 0,309, respectively, which were not significantly different from those of Lagreen and UCR 328. In this experiment the SII_{yield} was 0,476, also indicating a higher stress level in Exp 2 than in the previous experiment.

4.6.3. Pod yield

Pod yield (Table 27) showed parallel levels to those of seed yield. Under ww conditions in Exp 1 IT 18 formed the highest pod mass, while the same holds true for UCR 328 under wd stress. In Exp 2 TVu 12348 presented itself as a genotype with a low seed and pod yield. Just as in the seed yield results, pod mass was clearly lower in the wd treatment of both experiments than the control one.

	Experiment 1: Pod yield (g)		**Experiment 2:** Pod yield (g)	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	5,16 ± 1,45 **a**	0,65 ± 0,45 **a**	**-**	**-**
UCR 328	56,57 ± 3,28 **bc**	52,74 ± 2,19 **b**	14,22 ± 0,59 **cd**	9,78 ± 1,33 **c**
UCR 1340	53,58 ± 4,08 **bc**	46,26 ± 3,96 **b**	12,68 ± 0,95 **bc**	4,97 ± 0,63 **a**
IT 18	62,02 ± 1,38 **c**	44,09 ± 1,47 **b**	16,16 ± 1,38 **d**	6,27 ± 0,71 **ab**
UCR 386	54,63 ± 0,69 **bc**	47,23 ± 5,53 **b**	11,02 ± 1,42 **b**	5,71 ± 1,21 **ab**
Lagreen	51,11 ± 5,49 **b**	43,11 ± 0,98 **b**	11,06 ± 1,09 **bc**	8,65 ± 0,80 **bc**
Vita 7	**-**	**-**	**-**	**-**
TVu 12348	**-**	**-**	7,08 ± 0,79 **a**	6,10 ± 0,36 **ab**
IFH 27-8	**-**	**-**	10,56 ± 0,87 **b**	8,18 ± 0,57 **bc**
Mean	**47,18 ± 4,15**	**39,01 ± 3,79**	**11,83 ± 0,75**	**7,09 ± 0,39**

Table 27: Pod yield (means ± standard error; under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and 2 (N = 6). The same letters signify lack of difference within an experiment and column ($P \leq 0,05$). bs: before stress; se: stress end (maximum wd stress)

4.6.4. Single grain mass (SGM)

Single grain mass (SGM) (Table 28) varied among genotypes in both treatments and experiments and was affected differently by wd stress according to genotype. SGM ranged from 106 – 230 mg $seed^{-1}$ under ww conditions, and 48 to 190 mg $seed^{-1}$ under wd stress in Exp 1. In both cases the seeds of UCR 328 were the heaviest and those of Ex Ukwala the lightest. UCR 386 also had light seeds in this experiment. In UCR 386 drought stress increased SGM by 8% while it remained constant for IT 18. Otherwise the remaining

genotypes experienced a decline of SGM varying from 1 to 54%. In Exp 2 there was a similar picture regarding SGM under both conditions. UCR 328 had the heaviest seeds under both conditions, while IFH 27-8 produced relatively heavy seeds under ww conditions, but the heaviest in the stress treatment. Meanwhile UCR 386 again had the least heavy seeds under both conditions and TVu 12348 had the lighest seeds only in the stress treatment. Drought led to an increase of SGM in IT 18 (6%) and IFH 27-7 (35%), while all other genotypes experienced a decline from 3 – 19%. SGM in Exp 2 was lower (with the exception of Lagreen where it was similar in both experiments) than in Exp 1 under ww conditions, but higher in Exp 2 under wd conditions (Table 28).

	Experiment 1: Single grain mass (mg)		**Experiment 2:** Single grain mass (mg)	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	105,7 ± 5,0 **a**	48,1 ± 27,8 **a**	-	-
UCR 328	230,3 ± 4,0 **d**	190,2 ± 7,8 **c**	185,3 ± 2,6 **d**	180,3 ± 2,8 **e**
UCR 1340	124,5 ± 2,7 **b**	114,9 ± 7,8 **b**	109,9 ± 2,6 **b**	106,8 ± 4,9 **b**
IT 18	127,3 ± 1,7 **b**	127,6 ± 3,7 **b**	113,3 ± 3,5 **b**	120,6 ± 4,5 **c**
UCR 386	101,3 ± 1,9 **a**	108,9 ± 1,8 **b**	87,0 ± 2,5 **a**	77,8 ± 2,7 **a**
Lagreen	148,0 ± 4,5 **c**	146,3 ± 2,9 **b**	148,4 ± 3,2 **c**	139,3 ± 3,1 **d**
Vita 7	-	-	-	-
TVu 12348	-	-	102,6 ± 6,9 **b**	82,6 ± 5,5 **a**
IFH 27-8	-	-	138,8 ± 5,9 **c**	187,3 ± 7,6 **e**
Mean	**139,5 ± 9,1**	**122,6 ± 10,0**	**126,5 ± 5,0**	**127,9 ± 6,5**

Table 28: Mass of single grain (means ± standard error under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and 2 (N = 6). The same letters signify lack of difference within an experiment and column ($P \leq 0,05$). bs: before stress; se: stress end (maximum wd stress)

4.6.5. Harvest index (HI)

	Experiment 1: Harvest index, HI		**Experiment 2:** Harvest index, HI	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	0,02 ± 0,00 **a**	0,03 ± 0,00 **a**	-	-
UCR 328	0,44 ± 0,01 **d**	0,45 ± 0,01 **e**	0,51 ± 0,01 **d**	0,44 ± 0,06 **c**
UCR 1340	0,32 ± 0,03 **c**	0,38 ± 0,03 **d**	0,32 ± 0,02 **b**	0,29 ± 0,03 **b**
IT 18	0,46 ± 0,01 **d**	0,45 ± 0,01 **e**	0,48 ± 0,02 **cd**	0,29 ± 0,04 **b**
UCR 386	0,28 ± 0,01 **b**	0,21 ± 0,02 **b**	0,28 ± 0,04 **ab**	0,09 ± 0,03 **a**
Lagreen	0,33 ± 0,02 **c**	0,31 ± 0,02 **c**	0,33 ± 0,01 **b**	0,28 ± 0,02 **b**
Vita 7	-	-	-	-
TVu 12348	-	-	0,23 ± 0,02 **a**	0,21 ± 0,04 **b**
IFH 27-8	-	-	0,42 ± 0,04 **c**	0,41 ± 0,04 **c**
Mean	**0,31 ± 0,03**	**0,30 ± 0,03**	**0,36 ± 0,03**	**0,29 ± 0,02**

Table 29: Harvest index (means ± standard error) under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and 2 (N = 6). Within each column, means followed by the same letter do not differ significantly ($P < 0.05$). bs: before stress; se: stress end (maximum wd stress)

Harvest index (HI), the amount of DM partitioned to seeds (economic yield) relative to the shoot biomass, ranged in Exp 1 from very low in Ex Ukwala (0,02) to high (0,44 – 0,46 in UCR 328 and IT 18) under ww conditions (Table 29), while it lay between 0,03 (Ex Ukwala) and 0,45 (UCR 328) in the wd treatment. Fifty percent of the genotypes experienced an increase (2 – 50%) of HI under wd stress, while it was the opposite (6 – 74% decline) for the other genotypes. In Exp 2 HI of the genotypes varied between 0,23 (TVu 12348) and 0,51 (UCR 328), and between 0,09 (UCR 386) and 0,41/0,44 (IFH 27-8/UCR 328) in the control and stress treatment, respectively. All genotypes decreased their HI by 2 (IFH 27-8) – 68% (UCR 386) under stress in this experiment.

4.6.6. Shelling out-turn

Shelling out-turn (the percentage of seed obtained from the harvested mature pods) showed significant variation among genotypes in both experiments and treatments (Table 30). In Exp 1 shelling out-turn was higher (2%) in the wd treatment (relative to the control) only for UCR 1340, similar to the control in Lagreen, and lower (1 – 6%) than the control treatment for the remaining four genotypes. The ranges were similar in both treatments in Exp 1 (68 – 83% shelling out-turn). In Exp 2 shelling out-turn was 74 – 91% under ww conditions and 62 – 93% in the stress treatment. In Exp 2 three genotypes had higher shelling out-turn (IT 18, TVu 12348 and IFH 27-8: 2 – 7%) under wd stress compared with the ww treatment, constant in Lagreen, and lower (3 – 16%) in all other genotypes. In both experiments and treatments UCR 386 had the lowest shelling out-turn, while UCR 328 had the highest shelling out-turn in both treatments and experiments, and IFH 27-8 also had the highest shelling out-turn in both treatments in experiment 2. The genotype mean (Table 30) value was higher in Exp 2 (both treatments) than in Exp 1.

	Experiment 1: Shelling out-turn (%)		**Experiment 2:** Shelling out-turn (%)	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	74,34 ± 2,03 **b**	68,35 ± 5,19 **a**	**-**	**-**
UCR 328	82,96 ± 0,90 **c**	81,18 ± 0,53 **c**	91,30 ± 2,21 **c**	82,24 ± 2,31 **c**
UCR 1340	74,39 ± 1,82 **b**	76,79 ± 0,62 **b**	75,46 ± 2,17 **a**	71,18 ± 2,16 **b**
IT 18	78,30 ± 1,72 **bc**	75,76 ± 0,46 **b**	78,84 ± 3,02 **ab**	80,75 ± 4,24 **c**
UCR 386	68,90 ± 2,27 **a**	67,75 ± 0,68 **a**	77,49 ± 5,04 **a**	61,67 ± 2,66 **a**
Lagreen	78,25 ± 0,66 **bc**	78,98 ± 1,26 **bc**	78,44 ± 0,82 **ab**	78,14 ± 0,82 **bc**
Vita 7	**-**	**-**	**-**	**-**
TVu 12348	**-**	**-**	74,19 ± 2,67 **a**	76,19 ± 1,25 **bc**
IFH 27-8	**-**	**-**	86,26 ± 1,87 **bc**	93,01 ± 2,57 **d**
Mean	**76,19 ± 1,09**	**68,35 ± 1,15**	**80,28 ± 1,33**	**77,60 ± 1,65**

Table 30: Shelling out-turn (means ± standard error) under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and 2 (N = 6). The same letters signify lack of difference within an experiment and column ($P \leq 0,05$).

4.7. Relationships among traits

4.7.1. Correlations among gas exchange traits

Relationships under well-watered (ww) conditions among gas exchange traits and ETE are shown in Table A13 (Appendix).

As expected, leaf transpiration rate (E) under ww conditions in Exp 1 was strongly positively correlated with net photosynthetic rate (P_N) and stomatal conductance (g_s). E was also strongly, but negatively correlated with the ratio P_N to g_s (P_N/g_s) and intrinsic transpiration efficiency (TE_i), that is, the amount of CO_2 fixed to every unit water lost through transpiration (all at the probability level $P \leq 0.01$). P_N, a gas exchange process intrinsically coupled to E through the fact that both need stomata to occur, was highly related to C_i and moderately to g_s and negatively to P_N/g_s and TE_i.

Positive correlations also existed between g_s and TE_i and P_N/g_s. Negative ones were found between g_s and P_N/g_s, as well as g_s and TE_i. It is interesting to note that g_s was the only gas exchange characteristic that was related to evapotranspiration efficiency (ETE). Besides, P_N/g_s was highly positively related to TE_i. TE_i had no significant linear correlation with ETE. In Exp 2 under ww conditions, high positive correlation coefficients existed among P_N, E and g_s, while negative one were found for P_N and g_s to P_N/g_s, and for E to TE_i. All gas exchange traits in this experiment displayed no relationship to ETE.

Under wd conditions in all experiments, stress appears to have altered the relationship among some gas exchange parameters, as well as the magnitude of these correlations. E was positively correlated to P_N, g_s and P_N/g_s only. No other relations could be established among gas exchange parameters. In Exp 2, More relations existed among gas exchange traits under wd conditions. Highly positive correlations existed among P_N, E and g_s, while the relationship of P_N, E and g_s to TE_i and P_N/g_s were negative. Only E was correlated to ETE (negatively), but the magnitude of this relationship was low.

4.7.2. Correlations among gas exchange, evapotranspiration efficiency, biomass traits, leaf temperature and yield

For brevity, linear relationships among traits mainly in Exp 1 and Exp 2 are presented here. Under ww conditions P_N had no relationship to LA, SLA, LMR, SMLR, RGR and NAR,

whereas E was negatively correlated to LMR and SMLR and g_s correlated to SLA, SMLR and RGR. P_N/g_s was related to SLA, LMR, SMLR, SMR and RGR, while TE_i had comparable correlations to these traits except RGR.

Of the gas exchange traits g_s and P_N/g_s were related to most yield components under ww conditions in Exp 1, the exception being P_N/g_s and HI. TE_i was related only with number of seeds and pods per plant. In Exp 2, it was only P_N/g_s with pod yield ($R = 0,345$; $P \leq 0,05$), seed yield ($R = 0,350$; $P \leq 0,05$) and SGM ($R = 0,408$; $P \leq 0,01$). TE_i was not related to any yield components in Exp 2 under ww conditions. All the correlation coefficients among gas exchange traits and yield components were relatively low in Exp 2.

Under wd stress, the relationships between gas exchange traits and yield components became weaker (Exp 1) or even disappeared (Exp 2).

ETE (se) was positively correlated with seed and pod yield, and SGM, but not with HI in Exp 1 under ww conditions. ETE at maturity was negatively correlated with number of seeds $plant^{-1}$ ($R = -0,509$; $P \leq 0,05$) and HI ($R = -0,435$; $P \leq 0,05$) only. In Exp 2, ETE (se) was related with all yield components, although only weak. ETE at maturity was not related to any yield components. The relationships of ETE (se) to most yield components disappeared under wd stress so that ETE was only correlated with SGM ($R = 0,420$; $P \leq 0,05$) in Exp 1. The same applied to Exp 2. Under wd stress, ETE at maturity was not related to any yield components in both experiments.

SMLR under ww conditions was related only with pod yield in Exp 1, but with all yield components in Exp 2. Water deficit stress in Exp 2 led to a tightening of the relationship between SMLR and yield components, except with number of seeds and pods, where the relationship insignificant. In Exp 2, SMLR had weaker relationships to yield components.
In Exp 1 under ww conditions, ΔT was negatively correlated with ETE, WUE (maturity) SGM and HI, but negatively with time to maturity (Table A16). In Exp 2, ΔT was positively related with time to anthesis, leaf shedding score (LSS) and TE_i (Table A17, Appendix). Under wd conditions, ΔT in Exp 1 was related with more traits than under ww conditions and most correlations coefficients were moderate to high. Most notable relations are negative correlation coefficients between ΔT and SMLR, RWC, time from anthesis maturity, all yield components studied and the positive correlations to LSS, time to anthesis and time to

maturity. In Exp 2, ΔT was negatively correlated with ETE, SMLR, RWC, CMS, most yield components, WUE (maturity), time from anthesis to maturity, ETE and RWC, but positively with P_N/g_s, time to anthesis, LSS and TE_i. LSS was consistently negatively related with HI (Table A17, Appendix) under both ww and wd conditions.

5. DISCUSSION

5.1. Gas exchange

Generally, instantaneous P_N and E have a weakness because they are values for a particular moment, influenced by conditions prevailing at that moment. A better measurement of E would be the cumulative values (based on daily weighing of pots) which has been used in various reports (e. g. Kholová *et al*. 2009; Ray and Sinclair, 1998; Sinclair and Ludlow, 1986) and was found to give a reliable measure of the degree of drought tolerance (Kholová *et al*. 2009).

The complex reaction of the net photosynthetic rate (P_N) to drought involves constraints at different sites in the leaf depending on the stage of development of the leaf and the plant, and is among the early processes affected by water deficit (Chaves, 1991; Chaves *et al.*, 2009, Lawlor and Tezara, 2009). In recent years there has been a heated debate (Tezara *et al.*, 1999; Cornic, 2000; Flexas *et al.*, 2004; Bota *et al.*, 2004; Flexas *et al.*, 2006b) on whether the effect of water deficit is mainly due to stomatal responses (stomatal closure) or metabolic reaction (mesophyll effects). The P_N rates obtained in these studies under ww conditions partly agree with those in the literature (Anyia and Herzog, 2003; Garg *et al.*, 2005; Zegada-Lizarazu *et al.*, 2006; Hamidou *et al.*, 2007). In the three experiments, mean P_N under ww conditions ranged between 6 and 10 µmol m^{-2} s^{-1}, values lower than those found by Anyia (2000) working with most of the genotypes used in the present study. Other studies with cowpea (Sangakkara *et al.*, 2000; Turner *et al.*, 1984; Katayama *et al.*, 1998) also found higher P_N values. In soyabean, however, Huck *et al.*, 1983 found actual P_N to be appreciably lower than maximum for a larger part of the day, even when the soil water content was kept at field capacity. Differences between these results found in the present studies and those presented in the literature under ww conditions can be attributed to differences in experimental conditions, for example, Anyia (2000) carried out experiments in a growth chamber with fully controlled growth conditions. Working with cowpeas in pots in the greenhouse, Lopez *et al.* (1987) found similar P_N values as in our studies and Küppers *et al.* (1988) measuring gas exchange in the greenhouse at a photosynthetic photon flux density of 800 µmol m^{-2} s^{-1} similar to ours found maximum P_N values of 16 µmol m^{-2} s^{-1}, comparable to those of some genotypes like UCR 386, UCR 328, UCR 1340 and TVu 12348 in the present studies. Discrepancies between various experiments are particularly high when comparing results of field experiments and greenhouse experiments such as ours. Plants under field conditions generally

receive higher photosynthetically active radiation, resulting in higher P_N. However, this can, under some circumstances, also lead to the damage of the photosynthetic apparatus of C_3 plants like cowpeas if it is much higher than the saturation levels, especially under stress conditions. P_N under ww conditions was not consistent in the three experiments, a likely indication of the interaction of the experimental conditions (year) with the genotypes, because the greenhouse conditions could not be fully controlled the effects of the different winters (Exp 1 and Exp 2) could have influenced P_N differently in the different years. In particular Ex Ukwala and UCR 1340 showed much higher genotype X environment interactions. UCR 386 is a genotype with high P_N, as also found by Anyia (2002). In these studies it had high P_N only before stress – three weeks later plummeting to only one third to one fifth of P_N bs. Although it is tempting to seek a clarification in leaf aging, this can be discredited because gas exchange measurements were carried out only on the youngest, uppermost fully developed leaflets. However, the question of age of leaves has credence only in that the ages of the measured leaves was not determined using an exact method, but was only estimated according to position and appearance. This phenomenon of UCR 386 can be ascribed to observed, large but uneven leaves which made it difficult to reliably measure gas exchange at the onset of flowering. A similar problem was encountered in the genotype Vita 7, with its very thick veins.

Water deficit clearly led to reduction of P_N in all genotypes. In fact, P_N was related to RWC of the leaves under both ww and wd conditions in Exp 1 ($R = 0,65$; $P < 0,01$ and $R = 0,46$; $P < 0,05$, respectively) and Exp 3 ($R = 0,40$; $P < 0,05$ and $R = 0,61$; $P < 0,01$, respectively), but not in Exp 2 under both conditions. It is not clear why P_N was not related to RWC in Exp 2, but it might be an indication that factors other than just wd stress, such as vapour pressure deficit (VPD), or effects of pest pressure, were at play affecting responses of P_N. In all the experiments, UCR 386, UCR 328 and IFH 27-8 maintained relatively high P_N under wd, being affected relatively less by it than the other genotypes. This maybe a pointer to a better tolerance of P_N of these genotypes to wd stress. Significant and fast changes in the photosynthetic rates after resumption of full irrigation illustrate how quickly the cowpea plants responded to alleviation of wd stress, a factor also important when breeding for drought tolerance.

It is evident that P_N was mainly affect by stomatal closure because P_N correlated positively with g_s (Table A13). This came as no surprise since it is well-known that cowpea has a tight

control of gas exchange through its very wd sensitive stomata (Souza *et al.*, 2004; Bates and Hall, 1981). Other C_3 plants also generally respond quite early to mild and moderate wd stress through stomatal closure (Flexas *et al.*, 2004; Cornic and Massacci, 1996). However, the influence of wd stress was more marked on E than on P_N, where generally higher relative reduction took place. UCR 328, UCR 386 and IFH 27-8 were among those with the least reduction of E. These genotypes were probably able to maintain partially open stomata, leading to maintenance of E and enabling diffusion of CO_2, thus perpetuating P_N during stress. The role of g_s in E is also underscored by the positive relationship between these two traits (Table A13) in Exp 1. At least equally high linear relationships [R = 0,72 (ww) and 0,91 (wd); P < 0,01] were established between these two characteristics in Exp 2. P_N and E are important factors for DM accumulation and growth and indirectly for seed yield (Moss and Musgrave, 1971; Fageria, *et al.*, 2006) integrated over growth intervals of the plants. While, on the one hand, mean P_N in Exp 1 was reduced by 58 % under wd stress, g_s was reduced by 86 % indicating the overriding role of stomatal closure. In Exp 2, on the other hand, mean P_N experienced a scaledown of 39 % as opposed to the decrease of 23 % in mean g_s. The results in Exp 1 regarding reduction of P_N and g_s, agree with those obtained by Hall *et al* (1992) also working with cowpea. The results obtained in Exp 2 do not agree with the results of Hall *et al.* (1992), but Emendack (2007), working with *Sorghum bicolor* and *Panicum miliaceum* genotypes, obtained results similar to those in Exp 2. Emendack (2007) attributed this discrepancy to differences in stress intensity and stress duration. In this study, differences might have been brought about by deviations in both stress intensity and duration, but perhaps more importantly by the interaction with the environment, especially the pressure of pests (red spider mites, thrips and white flies) and the control measures against these pests in Exp 2. Another important factor impacting on the response of P_N to stress is leaf thickness. Calculated on unit leaf area basis, thicker leaves generally have higher P_N because they contain more components of the photosynthetic apparatus. Yet Hoffmann-Bahnsen (1996) concluded that cowpeas achieve their maximum P_N at the end of the main flower flush, which might also explain the differences between genotypes. It is not only stomatal closure that is important for gas exchange in legumes, but also the duration for stomata to become fully opened or closed, stomatal density and leaf movements (paraheliotropism) in reaction to stress and light, which have been found to vary with genotype in cowpea (Sekiya and Yano, 2008; Shackel and Hall, 1979), *Phaseolus vulgaris* (Lizana *et al.*, 2006) and *Glycine max* (Kao and Forseth, 1998; Kao and Forseth, 1991; Rosa *et al.*, 1991). Irradiance also plays a role in the response of gas exchange of the plants, especially in view of the PPFD during

measurement and that at which the plants grew (Lawlor and Tezara, 2009). This could possibly have affected the short-term gas exchange responses, leading to these major differences.

Regarding stress effects it is now widely accepted that single gas exchange traits on their own might not adequately explain the response to wd stress, which is why the trait intrinsic transpiration efficiency (TE_i), that is P_N/E (the amount of CO_2 fixed for every unit of H_2O transpired), was determined in this study. TE_i values in both treatments differed in all three experiments, pointing towards possible genotype X environment interactions.

Generally, TE_i was, as expected, higher under wd stress than under ww conditions. It is recognised that E is usually more affected by the reduction of the stomatal aperture (g_s) than is P_n, leading to an improvement of TE_i. However, the variation between genotypes used in this study in the relative increase of TE_i under wd stress might be an indication of differences in stomatal control and other mechanisms affecting TE_i. Recently, a gene (named ERECTA) contolling TE_i through regulating stomatal density, g_s and mesophyll development was reported in *Arabidopsis thaliana* (Masle *et al.*, 2005), thus regulating not only P_N but also E. One parameter related to P_N/E that expresses the regulation through ERECTA very well is the ratio P_N/g_s, which is considered by some (van den Boogaard *et al.*, 1997; Martin and Ruiz-Torres, 1992; Morgan and LeCain, 1991) to be the "real" TE_i and a better trait (since more stable) than P_N/E. The relative increase of P_N/g_s under wd stress was much higher in Exp 1 and Exp 3 than in Exp 2. In fact, only two genotypes (Ex Ukwala and UCR 328) had an increase, while the rest had a reduction of P_N/g_s. This might have something to do with the environmental conditions (pest pressure/control measures, light, temperature) alluded to earlier. Despite this, the stability that might be expected was not reflected in these studies, partly because there was no discernible consistency of genotype rankings among the three experiments.

According to correlations, the effect of g_s on P_N/g_s is clear in the three experiments (for example in Exp 2 R = -0,73 and -0,79; $P < 0,01$ under ww and wd conditions, respectively). On the other hand, g_s has moderate linear relationship to TE_i only under wd stress in Exp 2 and Exp 3, but no relationship between the two traits could be established in Exp 1.

5.2. Water use, evapotranspiration efficiency and water-use efficiency

Stanhill (1986) observed that ETE (WUE) rose considerably as atmospheric demand went up. The R^2 value was relatively high indicating a direct relationship between ETE of these experiments and DM production. This, therefore, possibly demonstrates an association between ETE and biomass production under varying soil water conditions that is conservative (Tolk and Howell, 2009). The variations among experiments might be dependent on genotype (Hanks, 1983), too low nutrient levels, too high available water or too high leaf density (de Wit, 1958), agronomic management and time of sampling biomass (Tolk and Howell, 2009).

An interesting finding was the negative correlation between g_s and ETE under adequate irrigation and wd stress in Exp 1, though it was non-significant, but still negative, in Exp 2. Although it is clear that this relationship does not necessarily imply causality, Hufstetler *et al.* (2007), who also reported a similar correlation in cotton and soyabean as established in the present studies, have speculated on the mechanistic link existing between these two traits.

5.3. Growth and biomass allocation

During the vegetative stage, water deficit stress reduces total plant biomass (DM). DM, shown to be linearly related to yield, can limit yield potential starting early in the growing season. Therefore, stress should be avoided early in the season, but especially during the generative and early phases of the reproductive stages.

In this section biomass, leaf area, SLA, LMR stem length, SMLR and SMR are discussed. One of the first plant traits to be negatively affected by water deficit stress is shoot growth (Hsiao, 1973; Neumann, 2008). Biomass accumulation was reduced in all genotypes, but with variation among genotypes in all experiments. In Exp 1 the mean dry matter of the shoot (DM) under wd was only 37 % of the ww treatment, in Exp 2 it was 53 %. Although the effect of wd stress appears to be more dramatic in Exp 1, the absolute mean DM was three times higher in Exp 1 than in Exp 2. While the G x E effect on DM production might have played a significant role in these experiments, the very low DM in Exp 2 might be an indication of other factors having a further effect on growth. As already mentioned in the gas exchange section, there was, perhaps, an effect also of pest infestation and the reaction of the genotypes to the effected control measures. Ex Ukwala and IT 18 had the lowest DM

reduction under stress (53 % and 58 %, respectively), while the rest had a DM reduction of 66 %. In Exp 2, the DM reduction was much more differentiated, but still with Ex Ukwala being among those genotypes having the lowest DM reduction under stress (among those genotypes common to both experiments), in contrast to the findings of Anyia (2001). Of the three new genotypes in Exp 2, wd stress led to a relatively low DM reduction especially in TVu 12348 and IFH 27-8. Besides, the response of DM production to wd stress in these two genotypes, there could be an indication of the tolerance of the two genotypes to pest infestation and/or to control measures. In this vein, Khan *et al*. (2009) suggested disease and pest resistance as crucial traits under drought stress, since diseases and pests lead to additional losses under wd stress and those genotypes exhibiting higher tolerance do not have these losses. Dadson *et al* (2005) in their work with cowpea, also pointed out that those genotypes with the highest drought tolerance in terms of DM production and yield were also resistant to a number of diseases and pests. The importance of maintenance of biomass accumulation lies in the fact that a strong DM decrease limits potential yield of the plant.

The results of all genotypes show clear effects of water deficit (wd) on DM accumulation and partitioning, leaf area (LA) and stem length compared with the ww treatment, but there were variations between experiments. DM accumulation was affected to a higher extent in Exp 1 than Exp 2 when using data of plants from planting to se. However, DM accumulation in the intervals (stress begin to stress end) exhibits a similarity in the effect of wd – a reduction of – 62 % (Exp 1) and 61 % (Exp 2), but a much lower reduction (32 %) in Exp 3. This is a likely reflection of the fact that the plants in this experiment were younger than in the previous two experiments. Comparing all three experiments, there is no clear consistency among genotypes regarding the behaviour of biomass accumulation. However, Ex Ukwala (Exp 1 and Exp 2) and IT 18 (Exp 1 and Exp 3) appear to reduce their biomass less than other genotypes under wd stress. On the other side, UCR 1340 might be a genotype which reduces its biomass much more than any other genotype included in this study. The significance of biomass accumulation lies in the fact that higher DM accumulation generally leads to a higher yield potential (Blum, 2000; Loss *et al.*, 1997). Contrary to this fact, Jamieson *et al.* (1984) demonstrated that in another grain legume, field peas (*Pisum sativum*), yield variation under drought conditions was under the control of changes in harvest index (HI), that is there was relatively less change in total biomass than in grain yield.

The role of leaf area (LA) in biomass accumulation is underlined by the relationship of the two traits under both water replete and wd stress conditions. LA at anthesis was positively correlated with shoot DM both at anthesis and maturity under stress but only at anthesis under adequate water in Exp 1 (Table A16) at both anthesis and maturity in both treatments in Exp 2 and at anthesis in Exp 3 under both treatments. This relationship was generally higher under adequate water, reflecting the disruption of biomass production caused by reduction of leaf area under stress due to accelerated leaf senescence and abscision, and reduced size per leaf.

The expected link between stem length and biomass could not be established at all in Exp 1. However, in Exp 2 stem length and shoot biomass were related under ww and wd conditions at anthesis and maturity, as well as in Exp 3 under both treatments at anthesis. These results concur with those reported by Villegas *et al.* (2001) in wheat. This was expected because stem length can give an indication of biomass accumulation and partitioning as it gives anchor and support to all the other shoot parts.

The link of LA to biomass accumulation and yield, and thereby the importance of LA accumulation, could be established by way of a moderate to high negative relationship between LA during anthesis (stress end) and yield and yield components, but a moderate to high positive correlation of LA to biomass under wd stress and adequate irrigation (Table A16, Appendix) in Exp 1 and Exp 2. Likoswe and Lawn (2008) found that cowpea, in comparison with soyabean (*Glycine max*) and pigeonpea (*Cajanus cajan*), discontinue leaf production and growth much earlier and at higher soil water potential, partially supporting the results obtained in the present studies.

In order to test the effect of wd stress during the stress interval only and thereby reduce the bias brought about by LA, biomass and stem length produced prior to wd stress induction, the interval LA, biomass (DM) and stem length were determined, i. e. the LA or DM or stem length attained specifically in the duration of the stress period.

In all three traits, it was not surprising that the interval values showed that stress had a greater impact than implied by the data for these traits from planting to stress end (0-se). Generally, LA_{int} was affected most by wd, followed by DM_{int}, and interval stem length was affected least. This is consistent with the findings of, for example, Boyer (1971), which demonstrated that growth is among the first plant parameters to be seriously by wd stress. Both LA and DM

are growth traits, with the former impacting on the latter. It was, however, unexpected, that StL_{int} would show such a lower response to wd stress than LA and DM accumulation – c. 10 percentage points lower than LA_{int} and DM_{int}. This probably is an indication that the genotypes invested more in the relative growth maintenance of the stem as a supporting structure under wd stress. To this end, Beaver *et al*. (1985) suggested that in another legume, soyabean, there is a tendency for plants to increase their stem DM content under wd stress, although their results were not consistent across years. The results in these demonstrate that stem mass ratio in all genotypes increased under the influence of wd stress, giving a plausible elucidation of the relatively lower stem length reduction (compared with LA_{int} and DM_{int}. Saraswati *et al.* (2004) found similar results in the dicot sweet potato (*Ipomoea batatas*).

5.4. Other morphophysiological traits

5.4.1. Leaf relative water content and leaf cell membrane stability

Regarding leaf RWC, one problem is that the RWC of the various genotypes under water deficit stress differ significantly, leading to the question whether the different responses were merely due to the different RWC but not to the wd stress per se. It would have been better to measure the different traits at a similar RWC for all genotypes. However, imposing stress *in situ* in such a way that all genotypes have similar RWC is very difficult, leaving only the possibility of cutting leaves from plants which might lead to leaf responses atypical of those on intact plants. RWC has been recommended (Agbocodo *et al.*, 2009) as a good physiological trait when examining cowpea genotypes for drought tolerance. However, in this regard there are contradicting results as to the utility of this trait in cowpea, with Cruz de Carvalho *et al.* (1998) reporting no consistency, while Slabbert *et al.* (2004) reported that it was a good trait to reliably differentiate cowpea genotypes under drought. In our studies age of plants and leaves and treatment affected RWC and it appears that drought tolerant genotypes, for example UCR 328, TVu 12348 and IFH 27-8, and maintained higher RWC under wd stress.Under wd stress, it was positively correlated with TE_i, P_N/g_s and ETE, but not to yield in Exp 1, only to ETE but to yield as well in Exp 2. Thus, there is no clear indication of the significance and reliability of RWC as a drought-tolerance indicator. More work is necessary to illuminate this trait in cowpea.

Cell injury and eventually cell death are known to occur under wd stress and may lead to leakiness of cells and poor recovery. As such, leakiness of cells can be used as a measure of deterioration or even loss of function of the plasmalemma. Leakiness has been found to be inversely correlated to ability to recover from water deficit stress (Leopold *et al.*, 1981).

In the study of Srinivasan *et al.* (1996) with the legumes groundnut (*Arachis hypogaea*) and soyabean (*Glycine max*) CMS was negatively correlated with SLA. While Labuschagne *et al.* (2008) found CMS to be a reliable method for determining the drought tolerance of various cowpea genotypes, Ismail and Hall (1999) and Thiaw and Hall (2004) found strong negative correlations between CMS and yield under heat stress. In wheat, Reynolds *et al.* (1994) and Saadalla *et al.* (1990) found that CMS was negatively correlated with seed yield. It can be inferred from our results and those cited above that these relationships indicate probable linkages between CMS and photosynthesis as well as other yield-influencing physiological traits, an intimation also recently made by Reynolds *et al.* (2009). Working with cowpea, Thiaw and Hall (2004) found that CMS had moderate heritability and they pointed out that CMS was determined by nuclear instead of maternal factors because heritabilities of different crosses were similar and that selection for high CMS in crosses can be expected to be effective in cowpea. The prospect that greater photosynthetic performance of high CMS genotypes (e.g. UCR 328 and IFH 27-8) maybe thereby associated with higher stability of PSII under stress conditions (Reynolds *et al.*, 1994; Srinivasan *et al.*, 1996) and other wd stress adaptive traits.

5.4.2. Leaf senescence and abscission

Leaf senescence and abscission are responses of the plant to wd stress, in order to reduce the transpiring leaf surface and thereby conserve soil water for later usage. As was found here in these studies and elsewhere in the literature (e. g. Semonov *et al.*, 2009; Akyeampong, 1985) there were genotypic variations for leaf senescence and abscission. The leaf shedding score (LSS) displayed a consistency as shown by no other trait examined in these studies. UCR 328 was very consistent with regard to leaf shedding in all three experiments under both ww and wd conditions, being very conservative in its leaf shedding. Under water replete (control) conditions, it shed only its primary leaves chiefly as a result of shading of the lower stem and leaves by the upper leaves. Under wd stress, this genotype continued growing very slowly, producing virtually no new leaves, but maintaining green stems. However, it maintained all its

hitherto (prior to imposition of wd stress) produced leaves, which remained green, and contrary to all other genotypes displayed almost no wilting. This interesting phenomenon as a drought-response mechanism was described previously by Mai-Kodomi *et al*. (1999a), who divided the drought tolerance of cowpeas in two groups based on leaf abscission, wilting and plant survival of genotypes – Type 1 and Type 2. Accordingly, UCR 328 has a Type 2 drought tolerance because it remained green during the stress period and continued slow growth of leaves under wd stress – contrary to Type 1 drought tolerance, where plants stop growth after the beginning of wd stress and show declining plant tissue turgidity, and their new trifoliates are tiny. Almost all parts gradually die almost at the same time. Type 2 wd tolerance, as it was exhibited by UCR 328, has clear advantages over Type 1 tolerance since it maintains photosynthesis and metabolism, albeit at a low level, and the plants remain alive for a longer time such that when water becomes available the plants are in a position to immediately respond to the improved water availability and can thus recover more quickly.

Contrary to UCR 328, Ex Ukwala consistently shed the highest number of leaves under both conditions. IT 18 and Vita 7 also shed substantial amounts of leaves under both treatments. Using LSS, these three genotypes appear to be very sensitive to wd stress. On the tolerant side, one might be tempted to put the genotypes TVu 12348 and IFH 27-8 in the Type 1 tolerance category, since they did lose some leaves. However, two factors make this classification uncertain. TVu 12348 was examined only in Exp 2 and the stress conditions were not long enough to observe the further development of leaf production and abscission.

While LSS was positively correlated with E and g_s, but negatively with TE_i and P_N/g_s under ww conditions (Table A17, Appendix) in Exp 1, it was negatively correlated with P_n, E and P_N/g_s under wd conditions. In Exp 2, LSS was not correlated to any gas exchange trait under both conditions. LSS was consistently negatively related to yield under both conditions in Exp 1 and Exp 2 (Table A17, Appendix). This underlines the role of LA (here the loss of it as represented by LSS) in the formation of yield and the importance of this trait as a drought resistance trait. In cereals, where this trait is usually examined as leaf rolling, senescence and death, it has been demonstrated that this trait is linked with yield (Clarke *et al*., 1991; Nachit *et al*., 1992). In cowpeas, Akyeampong (1985) found that leaf abscission was a pivotal mechanism linked to soil water conservation and yield. Since premature leaf shedding is not desirable, Kramer and Boyer (1995) pointed out that premature leaf senescence and

abscission should be reduced to a minimum through selection for genotypes whose leaves have a longer persistance under wd stress.

5.4.3. Leaf temperature

In contrast with the results of Rahman Khan *et al.* (2007), who found no variation among faba bean (*Vicia faba*) genotypes under wd stress, but under ww conditions, ΔT in our studies differentiated cowpea genotypes under both conditions, similar to the findings of Lopes and Reynolds (2010) in wheat. Whereas some reports on high tight relationships between ΔT (or leaf/canopy temperature) and g_s can be found in the literature, for example Rahman Khan *et al.* (2007) and Hirayama *et al.* (2006), no such relationship could be established in these studies with cowpea. A possible cause could be growth conditions in the greenhouse, especially relatively low photosynthetic photon flux density (PPFD) (Beyschlag and Eckstein, 2001) under which our plants were grown. This could possibly have led to stomatal heterogeneity (patchiness) (Laisk *et al.*, 1980; Mott and Buckley, 1998), thus disrupting the relationship between these two traits. The negative relationship between ΔT and RWC in all three experiments emphasizes the role of wd stress in increasing ΔT, corroborating the findings of Pandey *et al.* (1984b), who established a strong association between canopy temperature and leaf water potential. Besides the relationship of ΔT to RWC, further linear correlations also existed to LSS (positive), yield and HI (negative) (Table A20 and Table A21, Appendix), making ΔT (or leaf/canopy temperature) a significant potential selection characteristic for distinguishing between drought susceptible and drought tolerant cowpea genotypes. These results are reminiscent of similar findings reported in other grain legumes like chickpea (Kashiwagi *et al.*, 2008), cowpea (Chozin *et al.*, 2002) and faba bean (Rahman Khan *et al.*, 2007), but also in cereals like rice (Hirayama *et al.*, 2006) and wheat (Gutierrez *et al.*, 2010; Lopes and Reynolds, 2010; Pinto *et al.*, 2008; Fischer *et al.*, 1998). Lopes and Reynolds (2010) as well as Sponchiado *et al.* (1989) inferred strong associations between ΔT and root deeper roots in wheat and bean (*Phaseolus vulgaris*), respectively. The results obtained in our and other studies accentuate ΔT as a potentially valuable and robust physiological selection trait which is linked to important traits (such as yield) but that are difficult to measure or can only be determined at maturity. As a selection criterion ΔT has distinct merits, namely that it is inexpensive, simple, fast, many samples and genotypes can be tested, it is non-destructive, can be performed on individual plants as well as in/over canopies at any phenological stage as long as green leaves are still prevailing. ΔT has recently been used in precision phenotyping for gene discovery in wheat (Reynolds *et al.*, 2009). As an

integrative physiological trait, ΔT is a robust selection trait and in wheat has been demonstrated to raise genetic gains when used as a selection trait in high yield environments (Gutierrez *et al.*, 2010; Condon *et al.*, 2008) and, selecting for cooler canopies, the highest yielding lines could be identified (van Ginkel *et al.*, 2008). The robustness of this trait as a selection tool has been recently demonstrated by Pierre *et al.* (2010) in wheat.

Main stem length to stem mass ratio (SMLR) was one of the most consistent traits in all experiments for separating genotypes under wd stress. This probably is connected with the role the stem plays in accumulating, storing and redistributing water and nurients, which can play a significant role under drought stress and during recovery. Recently, Muchero *et al.* (2008) found in cowpea the utility of another aspect of the stem, stem greenness, as a consistent and reliable drought tolerance indicator trait, which was also strongly negatively associated with leaf senescence. Here SMLR was also negatively correlated with LSS under both wd and ww conditions. The beauty of this trait is that, despite it being destructively determined, it can be used long before maturity (in the vegetative up to anthesis phases) and it is simple and inexpensive to determine.

5.5. Yield and yield components

Generally, crop plants are regarded to be more sensitive to drought stress relative to their wild relatives, whether mild or severe, intermittent or only at the end of any one of the various phases. Some work with cowpea (e. g. Turk *et al*., 1980a) has indicated that yield can be reduced by drought at flowering.

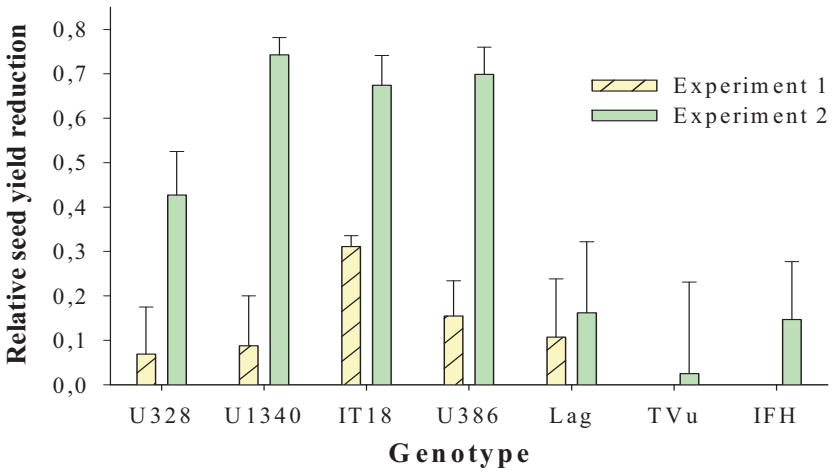

Fig. 18: Relative seed yield reduction (RYR) calculated as follows: **1 – (seed yield$_{stress}$/seed yield$_{nonstress}$)**

Seed yield and yield stability of the different genotypes shows that although TVu 12348 had a small relative yield reduction (Fig. 18), in contrast to UCR 1340, UCR 386, IT 18 and UCR 328 with much larger relative yield reduction values, it appears to have a low yield potential. UCR 328, Lagreen and IFH 27-8 have relatively low relative yield reduction and large seeds in both treatments. This seems to indicate that UCR 328 and Lagreen maintain their yield through a large seed yield and SGM compared to the other genotypes and by having a small seed yield and SGM reduction under stress. Due to the possible extreme photoperiodic reaction of Ex Ukwala and Vita 7 the yield of these two genotypes has not been included in this consideration. Genotypes with high yield potential generally out-yield those with lower yield potential under both ww and wd conditions (Blum, 1996).

The variation in seed yield displayed by the genotypes under ww conditions in both experiments shows a possible difference in yield potential of the genotypes. Ex Ukwala was thereby conspicuous, because it had an extremely low yield in Exp 1 and it, as well as Vita 7, did not flower at all in Exp 2. As already intimated earlier, this could be an indication that these two genotypes reacted particularly sensitive to the photoperiodic conditions in the greenhouse. Because DM is positively related to yield, Slafer *et al.* (1999) suggested that it is advantageous to select for increased plant biomass, but the height of the plants should not exceed a particular threshold depending on the species (since "too" tall plants tend to lodge and have a lower HI).

Generally, plant (crop) biomass is related with the integrated rates of photosynthesis over the whole plant (crop) growth period and in turn, DM is correlated with total plant (crop) yield, especially with harvest index (HI) (Fageria *et al.*, 2006). The leaf photosynthetic rate is influenced by the position of the leaf, plant nutritional status, plant water status, plant species, cultivar and plant growth stage (Fageria *et al.*, 2006). In crop plants higher yield generally not associated with higher photosynthetic rates, since different leaves in the canopy receive varying light intensities depending on the position of the leaf. Higher intrinsic rates of photosynthesis maybe associated with negative traits, for example higher respiratory activity (i. e. increased production and maintenance costs on account of a higher protein content) as indicated by Harris *et al.*, 1988 in groundnut (*Arachis hypogaea*).

Prolonged drought over any season can result in considerable yield loss. Crop WUE is sensitive to environmental conditions, with vapour pressure deficit being of notable significance by virtue of its effect on stomatal conductance (Day *et al.*, 1978; Lawlor *et al.*, 1981).

As crucial as WUE is, the enhancement of WUE alone is of no agronomic value if the yield the crop produces is too low. Rather, it may be more prudent to amend other morphophysiological traits in order to improve yield under drought conditions (Subbarao and Johansen, 2002; Sinclair and Muchow, 2001).

The reproductive traits flower and pod production and development, number of seeds pod^{-1}, as well as seed size contribute to seed yield. Water deficit stress can detrimentally influence all these parameters, however the extent varies with the timing of wd. Pandey *et al.* (1984a) reported for cowpea, soyabean, groundnut and mungbean that number of pods $plant^{-1}$ and number of seeds pod^{-1} were severely, while single seed mass was least affected by drought.

Considerable seed yield variability was found among genotypes and in the response of seed yield to wd stress. Mean yield loss was substantial (18 % in Exp 1 and 48 % in Exp 2), which was surprising, since mild to moderate wd stress was imposed at the onset of flowering. As such, a postponement of flowering and compensatory growth and flower production were expected as was reported for cowpea by Bala Subramanian and Maheswari (1991), Turk and Hall (1980b) and Turk *et al.* (1980). However, there are reports that water deficit can both delay or accelerate anthesis, reduce or extend pod-filling duration in cowpea (Sinclair *et al.*, 1987; Muchow, 1985; Lawn, 1982a) and in rapeseed (*Brassica napus*) (Tesfamariam *et al.*, 2010) – the orientation of the phenological response is contingent on the intensity of the wd stress (Craufurd *et al.*, 1996; Turk and Hall, 1980a). Assimilate supply probably limited the growth of early pods after relief from water deficit stress caused by relatively low photosynthetic rates, increased sink competition (Götz and Herzog, 2000) due to increased DM partitioning for leaf expansion, and relatively low LA per pod. Moreover, yield reduction corresponds more closely with light interception reduction at flowering/early seed filling than with leaf area reduction (Board *et al.*, 2010). Although there was a compensatory LA accumulation after release of wd stress, it obviously was not sufficient to be translated into a corresponding yield compensation. Anyia (2002) reported a minimal cowpea yield loss under moderate wd stress in a growth chamber. The levels of yield loss prevailing in our studies

were found by Anyia (2002) under severe wd stress (-750 hPa, contrary to the -350 to -400 hPa in our study). Thus it appears that the wd stress imposed here was more than moderate, bringing to the fore the question of yield by environment/experiment interaction. The wd stress in the greenhouse appears to be stronger (even if the soil water potential is relatively low) maybe due to high vapour pressure deficit (VPD), low photosynthetic photon flux density (PPFD), relatively low temperature across the whole ontogeny of the plants in our experiments and higher root proportion at the uppermost substrate layer. Nagarajah and Schulze (1983) found that low relative humidity in cowpea increases sensitivity to wd stress. Low temperature was reported to increase sensitivity to drought stress in beans (Kapitsimadi, 1988) which could have been the case in our experiments carried out in a greenhouse in the winter months and the temperature was relatively low for the growth and development of cowpea. As a result of restricted root volume in pots, a significant proportion of roots was in the topmost substrate layer, leading to a constant sensing of wd stress despite extractable water being available in deeper substrate layers. In these studies, cowpea yield response under wd stress could also have been influenced by yield potential, confirming results in other grain legumes (Silim and Saxena, 1993) and in pearl millet (Bidinger *et al.*, 1987)

The fact that seed and pod yield were affected by water deficit to similar magnitudes and the high regression coefficient between the two parameters show that seed yield reduction was influenced to a larger extent by pod growth and development. Although not recorded in these studies, more flower and pod abscission were observed in the wd treatment than under ww conditions. Thus, the final number of mature pods was lower in both experiments under wd, consistent with other results found in cowpea (e. g. Abayomi and Abidoye, 2009; Shouse *et al.*, 1981) and other grain legumes (e. g. Fang *et al.*, 2010; Leport *et al.*, 2006; Westgate and Peterson, 1993). Despite the fact that the overall number of seeds plant^{-1} was reduced under water deficit, the number of seeds pod^{-1} remained constant (11 seeds pod^{-1}) in Exp 1 and was only slightly reduced from 10 (ww) to 9 (wd) in Exp 2. Hence, the number of seeds pod^{-1} was relatively stable comparable to results of Lawn (1982b), but inconsistent with the results obtained by Tewolde *et al.* (1990) and Pandey *et al.* (1984a). SGM was also less affected by wd. The stability of SGM has also been previously reported by Tewolde *et al.* (1990), Pandey *et al.* (1984a) and Lawn (1982b).

Water deficit stress generally marginally increased HI as also reported by Craufurd and Wheeler (1999) and Lawn (1982b). There was a strong positive correlation of biomass

accumulated from flowering to maturity to seed yield and HI in Exp 1 (but not in Exp 2), (Table A20 and Table A21, Appendix) similar to the results of Craufurd and Wheeler (1999). The role of high yield potential under the influence of wd stress, coupled with a high yield stability, becomes evident especially in the genotype UCR 328. Compared with IT 18, which appears to also have a high yield potential but an unstable yield under wd stress, the latter maintains the highest yield under both ww and wd conditions, corroborated by the results of Anyia (2002). This is due to the maintenance of a high number of pods plant^{-1}, large seeds as evidenced by high SGM, high HI and shelling outturn. Despite TVu 12348 presenting the least yield loss due to wd and sustaining high HI (thus being drought resistant as also pointed out by Singh and Matsui, 2002 as well as Watanabe and Terao, 1998), it appears to have a low yield potential and its yield under wd is accordingly low, but might be a good parent in breeding to contribute yield stability under wd stress. When a genotype possesses high grain yield potential under ww conditions, this is not requisite for it to also produce improved yield under wd stress, as demonstrated by the genotype IT 18. As such, selection for high yield under optimum conditions will not necessarily be efficient for production under stress situations (Sio-Se Mardeh *et al.*, 2006). A genotype which displays a steady, reliable and relatively high yield under wd stress is valuable and beneficial both for direct utilisation in production and for breeding purposes.

Stomatal conductance manifested associations to seed yield and HI under both ww and wd conditions (Table A19 and Table A20, Appendix). Seed yield and HI were both consistently negatively correlated with SLA and LSS, while the relationship of SMLR and CMS to these two yield components was positive. Owing to these obtaining correlations in both experiments, the probability of them being causal is possibly high. Such a causal relationship of SLA to yield was reported recently by Ludwig and Asseng (2010) in wheat under hot and dry conditions. Genotypes with lower LSS produced produced higher yield and vice versa, reflected in the negative correlations between these two traits. This is due to the capacity of the low-LSS genotypes to accumulate more biomass under wd because more green leaf area was available for sustained photosynthesis as was shown experimentally in wheat (Christopher *et al.*, 2008; Foulkes *et al.*, 2007) and sorghum (Borrell *et al.*, 2000).

TE_i generally did not display any links with yield, whereas associations between ETE and yield existed mainly under adequate irrigation. This means that high ETE does not necessarily mean high yield under wd stress. That is why WUE, as used in our work, might be better than

ETE as a drought assessment criterion. Blum (2009) pleads for a shift away from ETE and TE_i to component traits and other criteria of water use and performance under wd stress, while Sadras *et al.* (2009) suggested using plasticity of phenological development and yield for the improvement of yield over various environmental conditions. Although not calculated as phenological plasticity in our studies, phenology per se, in the form of time to anthesis, time to maturity and time from anthesis to maturity, was found to be related to yield and HI (Table A19 and Table A20, Appendix) under both ww and wd conditions (strong in Exp 1, but weaker in Exp 2), whereby the former two traits were negatively, while the latter trait was positively correlated with yield and HI.

6. CONCLUSION

Drought in crop plants like cowpea has to be alleviated through a multifaceted approach, one of which is breeding of improved drought resistant cultivars. However, for such breeding programmes to be successful, it is imperative to study and characterise the morphological, physiological and agronomic responses of such "orphan" crops like cowpea which are of tremendous significance in the agriculture and diets of millions of people in the tropics and subtropics. Consequently, a number of morphophysiological and agronomic traits were considered in these studies and a number of important results were obtained. Based on these results several conclusions were made.

- For the nine genotypes water deficit stress effects were evident in all parameters measured.
- Under both ww and wd conditions variation was found for gas exchange (g_s, P_N, E and TE_i), WU, ETE, WUE, ΔT, leaf abscission, CMS and yield/yield components.
- Although the decline in soil water content led to decline in the gas exchange traits examined (g_s, P_N and E), the magnitude of decline varied according to the trait, genotype and experiment.
- P_N declined as a result of wd stress and possibly led to a decline in DM accumulation, which in turn probably induced increased leaf abscission (shedding). It is this leaf abscission and the concomitant leaf area reduction that effectively diminished biomass accumulation. The genotype UCR 328 was the only one with very low levels of leaf abscission under wd stress, although its biomass accumulation was low as well.
- ETE depended on genotype and interacted with experiments, making it necessary to determine ETE in various well-defined environments for every genotype.
- Stomatal conductance (g_s) and stem mass to stem length ratio (SMLR) might be potential parameters to characterise the ETE of cowpea genotypes since the former two traits showed consistent correlations with ETE in both treatments.
- Under wd conditions, most parameters were negatively affected, but evapotranspiration efficiency (ETE) of all genotypes improved – an indication that all levels of wd stress applied were relatively mild to moderate for the genotypes studied.
- Intrinsic transpiration efficiency (TE_i) and ETE may be weakly related, but their relationship was not nonsistent, making TE_i not particularly suitable nor reliable to

clarify and predict stomatal and non-stomatal constraints of wd stress on photosynthesis and ETE outcome in cowpea.

- Contrary to expectation ETE had only a weak negative linear relationship to specific leaf area (SLA).
- It appears that a relatively high SMLR before flowering could be used as a surrogate criterion for ETE for breeding purposes.
- CMS and SMLR might be potential parameters to characterise the drought resistance of cowpea genotypes and select for high yield under wd stress, since both were positively correlated with yield. There is also the possibility of using especially leaf or canopy temperature (ΔT), SMLR and CMS at the onset of flowering as surrogate traits for yield when screening for drought resistance.
- High ΔT and LSS impact on yield formation under wd stress negatively. Therefore, selection for lower ΔT and LSS in breeding programmes should lead to higher yield and harvest index under drought conditions. Both methods have the added advantages that they are simple, inexpensive, non-destructive, relatively fast to perform and can be applied at any phase of development well before maturity.
- The method of Fischer and Maurer (1978) to determine drought stress susceptibility appears to be a good method for determining drought intensity as a possible way of standardising wd stress induction, and genotypic ranking for drought resistance, especially when wd stress is moderate (and may be also severe). Using this approach, we were able to identify the same genotypes as drought resistant in different experiments.
- Unfortunately, with regard to breeding, some of those genotypes with consistently low yield reduction under stress (high wd resistance), for example TVu 12348, did not always yield the most under stress.
- TVu 12348, IFH 27-8 and UCR 328 were the most drought resistant genotypes in these studies. While TVu 12348 appears to a highly drought resistant, but generally low yielding genotype, IFH 27-8 has moderate drought resistance and moderate to high yield and UCR 328 has moderate to high drought resistance as well as high yield.
- Selection for high yield under optimum conditions will not necessarily be efficient for production under stress situations. As such it is of necessity to select under the given conditions in which the genotype is expected to be produced by farmers.

7. LITERATURE CITED

AATF (The African Agricultural Technology Foundation). 2007. Project 4: Cowpea Productivity Improvement (AATF Project Portfolio Briefs). www.aftechfound.org. Accessed on 15 December 2007

Abayomi, Y. A. and T. O. Abidoye. 2009. Evaluation of cowpea genotypes for soil moisture stress tolerance under screen house conditions. African Journal of Plant Science 3: 229 – 237

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

Agele, S. O., T. I. Ofuya and P. O. James. 2006. Effect of watering regimes on aphid infestation and performance of selected varieties of cowpea (*Vigna unguiculata* L. Walp.) in a humid rainforest zone of Nigeria. Crop Protection 25: 73 – 78

Akyeampong, E. 1985. Seed yield, water use, and water use efficiency of cowpea in response to drought stress at different developmental stages. PhD Thesis, Cornell University

Andersen, P. P., M. W. Lorch and M. W. Rosegrant. 1999. World food prospects: critical issues for the early twenty-first century, *In*: IFPR. Food Policy Report. Washington D. C.

Anyia, A. O. 2000. Genotypic variability and mid-season drought responses of cowpea under controlled environment. PhD Thesis at the Humboldt-Universität zu Berlin. Cuvillier Verlag, Göttingen

Anyia, A. O. and H. Herzog. 2004. Water-use efficiency, leaf area and gas exchange of cowpeas under mid-season drought. European Journal of Agronomy 20: 327 – 339

Araus, J. L. 1996. Integrative physiological criteria associated with yield potential. pp 150 – 167. *In*: M.P. Reynolds, S. Rajaram, and A. McNab (eds). Increasing yield potential in wheat: breaking the barriers. Mexico, D.F.: CIMMYT

Araus, J. L., J. Casadesus and J. Bort. 2001. Recent tools for the screening of physiological traits determining yield. pp 59 – 77. *In*: M. P. Reynolds, J. I. Ortiz-Monasterio and A. McNab (Eds). Application of physiology in wheat breeding. Mexico, D.F.: CIMMYT

Araus, J. L., G. A. Slafer, M. P. Reynolds and C. Royo. 2002. Plant breeding and drought in C_3 cereals: what should we breed for? Annals of Botany 89: 925 – 940

Bacon, M. A. 2004. Water use efficiency in plant biology. pp 1 – 26, *In*: M. A. Bacon (Ed.). Water use efficiency in plant biology. Blackwell Publishing Ltd, Oxford and CRC Press LLC, Boca Raton

Bala Subramanian, V. and M. Maheswari. 1991. Compensatory growth responses during reproductive phase of cowpea after relief of water stress. Journal of Agronomy and Crop Science 168: 85 – 90

Barbour, M. M., R. A. Fischer, K. D. Sayre and G. D. Farquhar. 2000. Oxygen isotope ratio of leaf and grain material correlates with stomatal conductance and grain yield in irrigated wheat. Australian Journal of Plant Physiology 27: 625 – 637

Barker, R., D. Dawe, T. P. Tuong, S. I. Buiyan and L. C. Guerra. 1999. The outlook for water resources in the year 2020: Challenges for research on water management in rice production. pp 96 – 109. *In*: D. V. Tran (Ed.), Assessment and orientation towards the 21st century. Proceedings of the 19th Session of the International rice Commission, September 7 – 9, 1998, Cairo, Egypt. Rome, FAO

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

Bates, L. M. and A. E. Hall. 1981. Stomatal closure with soil water depletion not associated with changes in bulk water status. Oecologia 50: 62 – 65

Beaver, J. S., R. L. Cooper and R. J. Martin. 1985. Dry matter accumulation and seed yield of determinate and indeterminate soybeans. Agronomy Journal 77: 675 – 679

Beyschlag, W. And J. Eckstein. 2001. Towards a causal analysis of stomatal patchiness: the role of stomatal size variability and hydrological heterogeneity. Acta Oecologica 22: 161 – 173

Bidinger, F. R., V. Mahalakshmi and G. D. P. Rao. 1987. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. II. Estimation of genotype response to stress. Australian Journal of Agricultural Research 38: 49 – 59

Blum, A. 2009. Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. Field Crops Research 112: 119 – 123

Blum, A. 2002. Drought Tolerance – is it a complex trait? pp 17 – 22. In: N. P. Saxena and J. C. O'Toole (Eds.). Field screening for drought tolerance in crop plants with emphasis on rice: Proceedings of an International Workshop on Field Screening for

Drought Tolerance in Rice, 11 – 14 Dec. 2000, ICRISAT, Patancheru, India and the Rockefeller Foundation, New York

Blum, A. 1996. Yield potential and drought resistance: Are they mutually exclusive? pp 90 – 100. *In* M. P. Reynolds *et al*. (Eds.) Increasing yield potential in wheat: Breaking the barriers. CIMMYT, Mexico, D.F.

Board, J. E., S. Kumudini, J. Omielan, E. Prior and C. S. Kahlon. 2010. Yield response of soybean to partial and total defoliation during the seed-filling period. Crop Science 50: 703 – 712

Borrell, A. K. and G. L. Hammer. 2000. Nitrogen dynamics and the physiological basis of stay-green in sorghum. Crop Science 40: 1295 – 1307

Bota, J., H. Medrano and J. Flexas. 2004. Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress? New Phytologist 162: 671 – 681

Boyer, J. S. 1982. Plant productivity and environment. Science 218: 443 – 448

Bradford, K. J. and T. C. Hsiao. 1982. Physiological responses to moderate water stress. pp 263 – 324. *In*: O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler (Eds). Encyclopedia of plant physiology Volume 12B. Springer-Verlag, Berlin

Bunting, A. H. and A. H. Kassam. 1988. Principles of crop water use, dry matter production and dry matter partitioning that govern choices of crops and systems. pp 43 – 61; *In*: F. R. Bidinger and C. Johansen (Eds). Drought research priorities for the dryland tropics. ICRISAT, Patancheru

Chaves, M. M. 1991. Effects of water deficits on carbon assimilation. Journal of Experimental Botany 42: 1 – 16

Chaves, M. M., J. Flexas and C. Pinheiro. 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. Annals of Botany 103: 551 – 560

Chinma, C. E., I. C. Alemede and I. G. Emelife. 2008. Physicochemical and functional properties of some Nigerian cowpea varieties. Pakistan Journal of Nutrition 7: 186 – 190

Chozin, M., J. O. Garner and C. E. Watson. 2002. Traits associated with drought resistances in cowpea. Jurnal Ilmu-Ilmu Pertanian Indonesia 4: 84 – 88

Christopher, J.T., A. M. Manschadi, G. L. Hammer and A. K. Borrell. 2008. Developmental and physiological traits associated with high yield and stay-green phenotype in wheat. Australian Journal of Agricultural Research 59: 354 – 364

Clarke, J. M., R. M. DePauw and T. F. Townley-Smith. 1991. Screening durum wheat germplasm for dry growing conditions: morphological and physiological criteria. Crop Science 31: 770 – 775

Condon, A. G. and A. E. Hall. 1997. Adaptation to diverse environments: variation in water-use efficiency within crop species. pp 79 – 116; *In*: L. E. Jackson (Ed.). Ecology in agriculture. Physiological Ecology Series. Academic Press, San Diego

Condon, A. G., M. P. Reynolds, G. J. Rebetzke, M. van Ginkel, R. Richards and G. Farquhar. 2008. Stomatal aperture-related traits as early generation selection criteria for high yield potential in bread wheat. pp 126 – 133. *In*: M. P. Reynolds, J. Pietragalla and H. Braun (Eds.). International Symposium on Wheat Yield Potential: Challenges to International Wheat Improvement. Mexico, D. F., Mexico: CIMMYT

Condon, A. G., R. A. Richards and G. D. Farquhar. 1987. Carbon isotope discrimonation is positively correlated with grain yield and dry matter production in field grown wheat. Crop Science 27: 996 – 1001

Condon, A. G., R. A. Richards, G. J. Rebetzke and G. D. Farquhar. 2004. Breeding for high water-use efficiency. Journal of Experimental Botany 55: 2447 – 2460

Cornic, G. 2000. Drought stress inhibits photosynthesis by decreasing stomatal aperture – not by affecting ATP synthesis. Trends in Plant Science 5: 187 – 188

Cornic, G. and A. Massacci. 1996. Leaf photosynthesis under drought. pp 347 – 366. *In*: N. R. Baker (Ed.). Photosynthesis and the environment. Dordrecht, Kluwer Academic Publishers.

Cowan, I. R. and G. D. Farquhar. 1977. Stomatal function in relation to leaf metabolism and environment. pp 471 – 505; *In*: D. H. Jennings (Ed.). Integration of activity in higher plants. Society for Experimental Biology symposium, Society for Experimental Biology, Cambridge

Craufurd, P. Q., A. Qi, R. H. Ellis, R. J. Summerfield and E. H. Roberts. 1996. Development in cowpea (*Vigna unguiculata*). II. Effect of temperature and saturation deficit on time to flowering in photoperiod-insensitive genotypes. Experimental Agriculture 32: 13 – 28

Craufurd, P. Q. and T. R. Wheeler. 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: 309 – 325

Cruz de Carvalho, M. H., D. Laffray and P. Louguet. 1998. Comparison of the physiological responses of *Phaseolus vulgaris* and *Vigna unguiculata* cultivars when submitted to drought conditions. Environmental and Experimental Botany 40: 197 – 207

Dadson, R. B., F. M. Hashem, I. Javaid, J. Joshi, A. L. Allen and T. E. Devine. 2005. Effect of water stress on the yield of cowpea (*Vigna unguiculata* L. Walp.) genotypes in the Delmarva Region of the United States. Journal of Agronomy and Crop Science 191: 210 – 217

Day, W., B. J. Legg, B. K. French, A. E. Johnston, D. W. Lawlor, W. D. C. Jeffers. 1978. Drought experiment using mobile shelters – effect of drought on barley yield, water-use and nutrient-uptake. Journal of Agricultural Science 91: 599 – 623

de Moody, B. E. 1985. Variability of different characteristics in Botswana cowpea germplasm. Tropical Grain Legume Bulletin 31: 1 – 4

de Wit, C. T. 1958. Transpiration and crop yields. Versl. Landbouwk. Onderz. No. 64.6. Inst. Biol. Chem. Res. Field Crops and Herbage, Wageningen, The Netherlands

Eamus, D., D. T. Taylor, C. M. O. Macinnis-Ng, S. Shanahan and L. de Silva. 2008. Comparing model predictions and experimental data for the response of stomatal conductance and guard cell tur leaf-to-air vapour pressure difference and temperature: feedback mechanisms are able to account for all observations. Plant, Cell and Environment 31: 269 – 277

Ehlers, W. 1997. Zum Transpirationskoeffizienten von Kulturpflanzen unter Feldbedingungen. Pflanzenbauwissenschaften 1: 97 – 108

Ehlers, J. D. and A. E. Hall. 1996. Genotypic classification of cowpea based on responses to heat and photoperiod. Crop Science 36: 673 – 679

Emendack, E. Y. 2007. Drought performance of millet (*Panicum miliaceum*) and sorghum (*Sorghum bicolor*). PhD Thesis at the Humboldt-Universität zu Berlin

Erice, G., S. Louahlia, J. J. Irigoyen, M. Sanchez-Diaz and J.-C. Avice. 2009. Biomass partitioning, morphology and water status of four alfalfa genotypes submitted to progressive drought and subsequent recovery. Journal of Plant Physiology 167: 114 – 120

Evans, J. R., T. D. Sharkey, J. A. Berry and G. D. Farquhar. 1986. Carbon isotope discrimination measured concurrently with gas exchange to investigate CO_2 diffusion in the leaves of higher plants. Australian Journal of Plant Physiology 13: 281 – 292

Fageria, N. K., V. C. Baligar and R. B. Clark. 2006. Physiology of crop production (Chapter 4: Photosynthesis and crop yield). Food Products Press, Binghamton

Fang, X., N. C. Turner, G. Yan, F. Li and K. H. M. Siddique. 2010. Flower numbers, pod production, pollen viability, and pistil function are reduced and flower and pod abortion increased in chickpea (*Cicer arietinum* L.) under terminal drought. Journal of Experimental Botany 61: 335 – 345

Farquhar, G. D. and R. A. Richards. 1984. Isotopic composition of plant carbon correlates with water use efficiency of wheat genotypes. Australian Journal of Plant Physiology 11: 539 – 553

Farquhar, G. D., J. R. Ehleringer and K. T. Hubick. 1989. Carbon-isotope discrimination and photosynthesis. Annual Review of Plant physiology and Plant Molecular Biology 40: 503 – 537

Fashakin, J. B. And J. I. Fasanya. 1988. Chemical composition and nutritive changes of some varieties of cowpea (*Vigna unguiculata*). 1. Some selected varieties from the International Institute of Tropical Agriculture, Ibadan, Nigeria. Tropical Science (UK) 28: 111 – 118

Fischer, R. A., D. Rees, K. O. Sayre, Z.-M. Lu, A. G. Condon and A. LarqueSaavedra. 1998. heat yield progress associated with higher stomatal conductance and photosynthetic ate and cooler canopies. Crop Science 38: 1467 – 1475

Fischer, R. A. and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Australian Journal of Agricultural Research 29: 897 – 912

Flexas, J., J. Bota, F. Loreto, G. Cornic and T. D. Sharkey. 2004. Diffussive and metabolic limitation to photosynthesis under drought and salinity in C_3 plants. Plant Biology 6: 269 – 279

Flexas, J., J. Bota, J. Galmés, H. Medrano and M. Ribas-Carbó. 2006a. Keeping a positive positive balance under adverse conditions: responses of photosynthesis and respiration to water stress. Physiologia Plantarum 127: 343 – 352 (Special Issue "Seasonally Dry Environments")

Flexas, J., M. Ribas-Carbó, J. Bota, J. Galmés, M. Henkle, S. Martínez-Canellas and H. Medrano. 2006b. Decreased Rubisco activity during water stress is not induced by decreased relative water, but related to conditions of low stomatal conductance and chloroplast CO_2 concentration. New Phytologist 172: 73 – 82

Foulkes, M. J., J. W. Snape, V. J. Shearman, M. P. Reynolds, O. Gaju, R. and Sylvester-Bradley 2007. Genetic progress in yield potential in wheat: recent advances and future prospects. Journal of Agricultural Science 145: 17 – 29

Franks, P. J. and G. D. Farquhar. 2007. The mechanical diversity of stomata and its significance in gas exchange control. Plant Physiology 143: 78 – 87

Fokar, M., H. T. Nguyen & A. Blum. 1998. Heat tolerance in spring wheat. I. Estimating cellular thermotolerance and its heritability. Euphytica 104: 1 – 8

Garg, B. K., U. Burman and S. Kathju. 2005. Comparative water relations, photosynthesis and nitrogen metabolism of arid legumes under water stress. Journal of Plant Biology 32: 83 – 93

Gebeyehu, S. 2006. Physiological response to drought stress of common bean (*Phaseolus vulgaris* L.) genotypes differing in drought resistance. PhD Thesis at the Justus-Liebig-Universität Giessen. Cuvillier Verlag, Göttingen

Gifford, R. M. and L. T. Evans. 1981. Photosynthesis, carbon partitioning, and yield. Annual Review of Plant Physiology 32: 485 – 509

Götz, K.-P. and H. Herzog. 2000. Distribution and utilization of ^{15}N in cowpeas injected into the stem under the influence of water deficit. Isotopes in Environment and Health Studies 36: 111 – 121

Gutierrez, M., M. P. Reynolds, W. R. Raun, M. L. Stone and A. R. Klatt. 2010. Spectral water indices for assessing yield in elite bread wheat genotypes under well-irrigated, water-stressed, and high-temperature conditions. Crop Science 50: 197 – 214

Gwathmey, C. O. and A. E. Hall. 1992. Adaptation to midseason drought of cowpea genotypes with contrasting senescence traits. Crop Science 32: 773 – 778

Hall, A. E., R. G. Mutters and G. D. Farquhar. 1992. Genotypic and drought-induced differences in carbon isotope discrimination and gas exchange of cowpea. Crop Science 32: 1 – 6

Hamidou, F., G. Zombre and S. Braconnier. 2007. Physiological and biochemical responses of cowpea genotypes to water stress under glasshouse and field conditions. Journal of Agronomy and Crop Science 193: 229 – 237

Hanks, R. J. 1983. Yield and water relationships: An overview. pp 393 – 411. *In*: H. M. Taylor et al. (Eds.). Limitations to efficient water use in crop production. ASA, CSSA and SSSA. Madison, WI

Harris, D., R. B. Mathews, R. C. Nageswara Rao and J. H. Williams. 1988. The physiological basis for yield between four genotypes of groundnut (*Arachis hypogaea*) in response to drought. III. Developmental processes. Experimental Agriculture 24: 215 – 226

Henshaw, F. O. 2008. Varietal differences in physical characteristics and proximate composition of cowpea (*Vigna unguiculata*). World Journal of Agricultural Sciences 4: 302 – 306

Herzog, H. 2002. Wassermangel: eine pflanzenbauliche Herausforderung. Mitteilung der Gesellschaft für Pflanzenbauwissenschaften 14: 14 – 19

Hiler, E. A., C. H. M. Van Bavel, M. M. Hossain and W. R. Jordan. 1972. Sensitivity of southern peas to plant water deficit at three growth stages. Agronomy Journal 64: 60 – 64

Hirayama, M., Y. Wada and H. Nemoto. 2006. Estimation of drought tolerance based on leaf temperature in upland rice breeding. Breeding Science 56: 47 – 54

Hoffmann-Bahnsen, R. 1996. Wassermangelstressempfindlichkeit bei fünf ausgewählten Tropischen und subtropischen Körnerleguminosen. Dissertation, Humboldt University of Berlin, Shaker Verlag, Aachen/Germany

Hsiao, T. C. 1973. Plant responses to water stress. Annual Review of Plant´Physiology 24: 519 – 570

Hubrick, K. T. and G. D. Farquhar. 1989. Carbon isotope discrimination and the ratio of carbon gained to water lost in cultivars of barley. Plant, Cell and Environment 12: 795 – 804

Hubrick, K. T., G. D. Farquhar and R. Shorter. 1986. Correlation between water use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. Australian Journal of Plant Physiology 13: 803 – 816

Huck, M. G. K. Ishihara, C. M. Peterson and T. Ushijima. 1983. Soybean adaptation to water stress at selected stages of growth. Plant Physiology 73: 422 – 427

Hufstetler, E. V., H. R. Boerma, T. E. Carter, Jr. and H. J. Earl. 2007. Genotypic variation for three physiological traits affecting drought tolerance in soybean. Crop Science 47: 25 – 35

IPCC. 2007. Intergovernmental Panel on Climate Change. Climate change 2007: The physical basis summary for policy makers, Cambridge. Cambridge University Press.

Ismail, A. M. and A. E. Hall. 1999. Reproductive-stage heat tolerance, leaf membrane thermostability and plant morphology in cowpea. Crop Science 39: 1762 – 1768

Jamieson, P. D., D. R. Wilson and R. Hanson. 1984. Analysis of responses of field peas to irrigation and sowing date. 2. Models of growth and water use. Proceedings of the Agronomy Society of New Zealand 14: 75 – 81

Jiang, Q., D. Roche, T. A. Monaco and D. Hole. 2006. Stomatal conductance is a key parameter to assess limitations to photosynthesis and growth potential in barley genotypes. Plant Biology 8: 515 – 521

Jones, H. G. 2007. Monitoring plant and soil water status: established and novel methods revisited and their relevance to studies of drought tolerance. Journal of Experimental Botany 58: 119 – 130; Special Issue (Integrated approaches to sustain and improve plant production under drought stress)

Jones, H. G. 2004. Irrigation scheduling: advantages and pitfalls of plant-based methods. Journal of Experimental Botany 55: 2427 – 2436

Jones, H. 2004. What is water use efficiency? pp 27 – 41, *In*: M. A. Bacon (Ed.). Water use efficiency in plant biology. Blackwell Publishing Ltd, Oxford and CRC Press LLC, Boca Raton

Jones, H. G. 1983. Estimation of an effective soil water potential at the root surface of transpiring plants. Plant, Cell and Environment 6: 671 – 674

Kao, W.-Y. and I. N. Forseth. 1998. Tropic leaf movements, photosynthetic gas exchange, leaf $\delta^{13}C$ and chlorophyll a fluorescence of three soybean species in response water availability. Plant, Cell and Environment 21: 1055 – 1062

Kao, W.-Y. and I. N. Forseth. 1991. The effects of nitrogen, light, and water availability on tropic leaf movements in soybean (*Glycine max*). Plant, Cell and Environment 14: 287 – 293

Kapitsimadi, C. M. 1988. Cultivar differences in the performance of bean seedlings at suboptimal temperatures. Annals of Botany 62: 677 – 685

Kashiwagi, J., L. Krishnamurty, H. D. Upadhyaya and P. M. Gaur. 2006. Rapid screening technique for canopy temperature status and its relevance to drought tolerance improvement in chickpea. SAT eJournal Volume 6; ejournal.icrisat.org

Katayama, K., O. Ito and T. P. Rao. 1998. Seedling characteristics and retention of current photosynthesis in leaves in relation to initial growth in pigeon pea (*Cajanus cajan* L. Millsp.) and cowpea (*Vigna chinensis* Endl.). Soil Science and Plant Nutrition 44: 477 – 480

Khan, H. R., J. G. Paull, K. H. M. Siddique and F. L. Stoddard. 2009. Faba bean breeding for drought-affected environments: A physiological and agronomic perspective. Field Crops Research 115: 279 – 286

Khan, M. A., I. Jacobsen and B. O. Eggum. 1979. Nutritive value of some improved varieties of legumes. Journal of the Science of Food and Agriculture 30: 395 – 400

Kholová, J., C. T. Hash, A. Kakkera, M. Kočová and V. Vadez. 2010. Constitutive water-conserving mechanisms are correlated with the terminal drought tolerance of pearl millet [*Pennisetum glaucum* (L.) R. Br.]. Journal of Experimental Borany 61: 369 – 377

Kirda, C., S. K. A. Danso and F. Zapata. 1989. Temporal water stress effects on nodulation, nitrogen accumulation and growth os soybean. Plant and Soil 120: 49 – 55

Kramer, P. J. and J. S. Boyer. 1995. Water relations of plants and soils. Academic Press, San Diego

Küppers, B. I. L., M. Küppers and E.-D. Schulze. 1988. Soil drying and its effect on leaf conductance and CO_2 assimilation of *Vigna unguiculata* L. Walp. I. The response to climatic factors and rate of soil drying in young plants. Oecologia 75: 99 – 104

Labuschagne, M. T., R. Verhoeven and M. Nkonanessi. 2008. Drought tolerance assessment of African cowpea accessions based on stomatal behaviour and cell membrane stability. Journal of Agricultural Science 146: 689 – 694

Laisk, A., V. Oja and K. Kull. 1980. Statistical distribution of apertures of *Vicia faba* and *Hordeum vulgare* and the *Spannungsphase* of stomatal opening. Journal of Experimental Botany 31: 40 – 58

Lambers, H., F. S. Chapin and T. L. Pons. 1998. Plant physiological ecology. Springer-Verlag Inc, New York

Lambers, H., M. L. Cambridge, H. Konings and T. L. Pons. 1989. Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague

Lawlor, D. W. and W. Tezara. 2009. Causes of decreased photosynthetic rate and metabolic capacity in water-deficient leaf cells: a critical evaluation of mechanisms and integration of processes. Annals of Botany 103: 561 – 579

Lawlor, D.W., W. Day, A. E. Johnston, B. J. Legg, K. J. Parkinson. 1981. Growth of spring barley under drought – crop development, photosynthesis, dry-matter accumulation and nutrient content. Journal of Agricultural Science 96: 167 – 186

Lawn, R. J. 1982a. Response of four grain legumes to water stress in south-eastern Queensland. I. Physiological response mechanisms. Australian Journal of Agricultural Research 33: 481 – 496

Lawn, R. J. 1982b. Response of four grain legumes to water stress in south-eastern Queensland. III. Dry matter production, yield and water use efficiency. Australian Journal of Agricultural Research 33: 511 – 521

Leopold, A. C., M. E. Musgrave and K. M. Williams. 1981. Solute leakage resulting from leaf dessication. Plant Physiology 68: 1222 – 1225

Leport, L., N. C. Turner, S. L. Davies and K. H. M. Siddique. 2006. Variation in pod production and abortion among chickpea cultivars under terminal drought. European Journal of Agronomy 24: 236 – 246

Levitt, J. 1980. Responses of plants to environmental stresses. Volume II. Water, radiation, salt and other stresses. Academic Press, New York.

Likoswe, A. A. and R. J. Lawn. 2008. Response to terminal water deficit stress of cowpea, pigeonpea, and soybean in pure stand and in competition. Australian Journal of Agricultural Research 59: 27 – 37

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

Lizana, C., M. Wentworth, J. P. Martinez, D. Villegas, R. Meneses, E. H. Murchie, C. Pastenes, B. Lercari, P. Vernieri, P. Horton, and M. Pinto. 2006. Differential adaptation of two varieties of common bean to abiotic stress. I. Effects of drought on yield and photosynthesis. Journal of Experimental Botany 57: 685 – 697

Loomis, R. S. and D. J. Connor. 1992. Crop ecology: productivity and management in agricultural systems. Cambridge University Press

Lopes, M. S. and M. P. Reynolds. 2010. Partitioning of assimilates to deeper roots is associated with cooler canopies and yield under drought in wheat. Functional Plant Biology 37: 147 – 156

Lopez, F. B., T. L. Setter and C. R. McDavid. 1987. Carbon dioxide and light responses of photosynthesis in cowpea and pigeonpea during water deficit and recovery. Plant Physiology 85: 990 – 995

Loss, S. P., K. H. M. Siddique and L. D. Martin. 1997. Adaptation of faba bean (*Vicia faba* L.) to dryland Mediterranean-type environments. II. Phenology, canopy development, radiation absorption and biomass partitioning. Field Crops Research 52: 29 – 41

Lugg, D. G. and T. R. Sinclair. 1971. Seasonal changes in photosynthesis of field-grown soybean leaflets. I. Relation of leaflets dimensions. Photosynthetica 15: 129 – 137

Mai-Kodomi, Y., B. B. Singh, O. Myers, Jr., J. H. Yopp, P. J. Gibson and T. Terao. 1999. Two mechanisms of drought tolerance in cowpea. Indian Journal of Genetics 59: 309 – 316

Mai-Kodomi, Y., B. B. Singh, T. Terao, O. Myers, Jr., J. H. Yopp and P. J. Gibson. 1999. Inheritance of drought tolerance in cowpea. Indian Journal of Genetics 59: 317 – 323

Martin, B., and N. A. Ruiz-Torres. 1992. Effects of water-deficit stress on photosynthesis, its components and component limitations, and on water use efficiency in wheat (*Triticum aestivum* L.). Plant Physiology 100: 733 – 739

Masle, J., S. R. Gilmore and G. D. Farquhar. 2005. The ERECTA gene regulates plant transpiration efficiency in *Arabidopsis*. Nature 436: 866 – 870

Medrano, H., J. M. Escalona, J. Bota, J. Gulias, and J. Flexas. 2002. Regulation of photosynthesis of C3 plants in response to progressive drought: stomatal conductance as a reference parameter. Annals of Botany 89: 895 – 905

Morgan, J. A. and D. R. LeCain. 1991. Leaf gas exchange and related leaf traits among 15 winter wheat genotypes. Crop Science 31: 443 – 448

Moss, D. N. And R. B. Musgrave. 1971. Photosynthesis and crop production. Advances in Agronomy 23: 317 – 336

Mott, K. A. And T. N. Buckley. 1998. Stomatal heterogeneity. Journal of Experimental Botany 49: 407 – 417

Muchero, W., J. D. Ehlers and P. A. Roberts. 2008. Seedling stage drought-induced phenotypes and drought-responsive genes in diverse cowpea genotypes. Crop Science 48: 541 – 552

Muchero, W., J. D. Ehlers, T. J. Close and P. A. Roberts. 2009. Mapping QTL for drought stress-induced premature senescence and maturity in cowpea [*Vigna unguiculata* (L.) Walp.]. Theoretical and Applied Genetics

Muchow, R. C. 1985. Phenology, seed yield and water use of grain legumes grown under different soil water regimes in a semi-arid tropical environment. Field Crops Research 11: 81 – 97

Munns, R. and R. A. Richards. 2007. Recent advances in breeding wheat for drought and salt stresses. pp 565 – 585 (Chapter 22). *In*: M. A. Junks, P. M. Hasegawa and S. M. Jain (Eds). Advances in molecular breeding toward drought and salt tolerant crops. Springer Publishing, Inc., Dordrecht

Nachit, M. M., M. E. Sorrells, R. W. Zobel, H. G. Gauch, W. R. Coffman and R. A. Fischer. 1992. Association of morpho-physiological traits with grain yield and components of genotype-environment interaction in durum wheat. Journal of Genetics and Breeding 46: 363 – 368

Nagarajah, S. and E.-D. Schulze. 1983. Responses of *Vigna unguiculata* (L.) Walp. to atmospheric and soil drought. Australian Journal of Plant Physiology 10: 385 – 394

Nageswara Rao, R. C. and G. C. Wright. 1994. Stability of the relationship between specific leaf area and carbon isotope discrimination across environments in peanut. Crop Science 34: 98 – 103

Nautiyal, P. C., N. R. Rachaputi and Y. C. Joshi. 2002. Moisture-deficit-induced changes in leaf-water content, leaf carbon exchange and biomass production in groundnut cultivars differing in specific leaf area. Field Crops Research 74: 67 – 79

Neumann, P. M. 2008. Coping mechanisms for crop plants in drought-prone environments. Annals of Botany 101: 901 – 907

NOAA (2006). National Oceanic and Atmospheric Administration (USA) at http://www.ncdc.noaa.gov/paleo/drought/drght_what.html; Accessed 29 May 2007

Ortiz, R. 1998. Cowpeas from Nigeria: a silent food revolution. Outlook On Agriculture 27: 125 – 128

OTA (1993). Office of Technology Assessment. Preparing for an uncertain climate, Volume 1. U. S. Government Printing Office, Washington, D. C.

Padulosi, S., N. Q. Ng and P. Perrino. 1997. Origin, taxonomy and morphology of *Vigna unguiculata* (L.) Walp.: 1 – 12. *In*: B. B. Singh, M. Raj, K. E. Dashiell and L. E. N. Jackai (Eds). Advances in cowpea research. IITA and JIRCAS, Ibadan, Nigeria

Pandey, R. K., W. A. T. Herrera and J. W. Pendleton. 1984a. Drought response of grain legumes under irrigation gradient. I. Yield and yield components. Agronomy Journal 76: 549 – 553

Pandey, R. K., W. A. T. Herrera and J. W. Pendleton. 1984b. Drought response of grain legumes under irrigation gradient. II. Plant water status and canopy temperature. Agronomy Journal 76: 553 – 557

Pettigrew, W. T. 2004. Physiological consequences of moisture deficit stress in cotton. Crop Science 44: 1265 – 1272

Pierre, C. S., J. Crossa, Y. Manes and M. P. Reynolds. 2010. Gene action of canopy temperature in bread wheat under diverse environments. Theoretical and Applied Genetics, In Press

Pinto, S., S. C. Chapman, C. L. McIntyre, R. Shorter and M. P. Reynolds. 2008. QTL for canopy temperature response related to yield in both heat and drought environments. *In*: Proceedings of the 11th International Wheat Genetics Symposium. Sydney, Australia: Sydney Unversity Press

Porter, D. R., H. T. Nguyen and J. J. Burke. 1995. Genetic control of acquired thermal tolerance in wheat. Euphytica 83: 153 – 157

Puangbut, D., S. Jogloy, N. Vorasoot, C. Akkasaeng, T. Kesmala, R. C. N. Rachaputi, G. C. Wright and A. Patanothai. 2009. Association of root dry weight, and transpiration efficiency of peanut genotypes under early season drought. Agricultural Water Management 96: 1460 – 1466

Purseglove, J. W. 1968. Tropical crops. Dicotyledons. Longmans, London

Ray, J. D. and T. R. Sinclair. 1998. The effect of pot size on growth and transpiration of maize and soybean during water deficit stress. Journal of Experimental Botany 49: 1381 – 1386

Rahman Khan, H. u., W. Link, T. J. Hocking and F. L. Stoddard. 2007. Evaluation of physiological traits for improvement of drought tolerance in faba bean (*Vicia faba* L.). Plant and Soil 292: 205 – 217

Reynolds, M. P., Y. Manes, A. Izanloo, P. Langridge. 2009. Phenotyping for physiological breeding and gene discovery in wheat. Annals of Applied Biology 155: 309 – 320

Reynolds, M. P., M. Balota, M. I. B. Delgado, I. Amani and R. A. Fischer. 1994. Physiological and morphological traits associated with spring wheat yield under hot irrigated conditions. Australian Journal of Plant Physiology 21: 717 – 730

Richards, R. A. 1996. Defining selection criteria to improve yield under drought. Plant Growth Regulation 20:157 – 166

Richards, R. A. 2006. Physiological traits used in the breeding of new cultivars for water-scarce environments. Agricultural Water Management 80: 197 – 211

Rosa, L. M., R. Dillenburg and I. N. Forseth. 1991. Responses of soybean leaf angle, photosynthesis and stomatal conductance to leaf and soil water potential. Annals of Botany 67: 51 – 58

Saadalla, M., J. F. Shanahan and J. S. Quick. 1990. Heat tolerance in winter wheat. II. Membrane thermostability and field performance. Crop Science 30: 1248 – 1251

Sadras, V. O., M. P. Reynolds, A. J. de la Vega, P. R. Petrie and R. Robinson. 2009. Phenotypic plasticity of yield and phenology in wheat, sunflower and grapevine. Field Crops Research 110: 242 – 250

Sanden, R. 1993. Blackeye varietal and irrigation cutoff trial. *In*: University of California dry Bean research – 1993 Progress Report, California Dry Bean Advisory Board, Dinuba, California pp. 120 – 121

Sangakkara, U. R., M. Frehner and J. Nösberger. 2000. Effect of soil moisture and potassium fertilizer on shoot water potential, photosynthesis and partitioning of carbon in mungbean and cowpea. Journal of Agronomy and Crop Science 185: 201 – 207

Saraswati, P., M. Johnston, R. Coventry and J. Holtum. 2004. Identification of drought tolerant sweet potato (*Ipomoea batatas* (L.) Lam) cultivars. 4th International Crop Science Congress, September 2004 in Brisbane,

Schindler, U., J. Steidl, L. Müller, F. Eulenstein and J. Thiere. 2007. Drought risk to agricultural land in Northeast and Central Germany. Journal of Plant Nutrition and Soil Science 170: 357 – 362

Sekiya, N. and K. Yano. 2008. Stomatal density of cowpea correlates with carbon isotope discrimination in different phosphorus, water and CO_2 environments. New Phytologist 179: 799 – 807

Semenov, M. A., P. Martre and P. D. Jamieson. 2009. Quantifying effects of simple wheat traits on yield in water-limited environments using a modelling approach. Agricultural and Forest Meteorology 149: 1095 – 1104

Serraj, R., T. R. Sinclair and L. C. Purcell. 1999. Symbiotic N_2 fixation response to drought. Journal of Experimental Botany 50: 143 – 155

Shackel, K. A. And A. E. Hall. 1979. Reversible leaf movements in relation to drought adaptation of cowpea, *Vigna unguiculata* (L.) Walp. Australian Journal of Plant Physiology 6: 265 – 276

Shouse, P., S. Dasberg, W. A. Jury and L. H. Stolzy. 1981. Growth stage water deficit effects on plant water potentials, dry matter production, seed yield and water use efficiency of field-grown cowpeas. Agronomy Journal 73: 36 – 41

Silim, S. N. and M. C. Saxena, 1993. Adaptation of spring-sown chickpea to the Mediterranean basin. II. Factors influencing yield under drought. Field Crops Research 34: 137 – 146

Silim, S. N. And M. C. Saxena. 1992. Comparative performance of some faba bean (*Vicia faba*) cultivars of contrasting plant types. 2. Growth and development in relation to yield. Journal of Agriculturural Sciences 118: 333 – 342

Sinclair, T. R. and M. M. Ludlow. 1986. Influence of soil water supply on the plant water balance of four tropical grain legumes. Australian Journal of Plant Physiology 13: 329 – 341

Sinclair, T. R. and R. C. Muchow. 2001. System analysis of plant traits to increase grain yield on limited water supplies. Agronomy Journal 93: 263 – 270

Sinclair, T. R., R. C. Muchow, J. M. Bennett and I. C. Hammond. 1987. Relative sensitivity of nitrogen and biomass accumulation to drought in field-grown soybean. Agronomy Journal 79: 986 – 991

Singh, B. B. 2005. Cowpea [*Vigna unguiculata* (L.) Walp]. pp. 117 – 162. *In:* R. J. Singh and P. P. Jauhar (Eds.). Genetic Resources, chromosome engineering and crop improvement. Volume 1, CRC Press, Boca Raton, USA

Singh, B. B. 1999. Breeding for improved quality. IITA Annual Report 1999, Project 11: 31 – 32

Singh, B. B., O. L. Chambliss and B. Sharma. 1997. Recent advances in cowpea breeding. p 30 – 49. *In*: B. B. Singh, M. Raj, K. E. Dashiell and L. E. N. Jackai (Eds). Advances in cowpea research. IITA and JIRCAS, Ibadan, Nigeria

Singh, B. B. and T. Matsui. 2002. Cowpea varieties for drought tolerance. pp 287 – 300. In: C. A. Fatokun, S. A. Tarawali, B. B. Singh, P. M. Kormawa and M. Tanò (Eds.). Challenges and opportunities for enhancing sustainable cowpea production. Proceedings of the World Cowpea Conference III held at the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, 4 – 8 September 2000

Sio-Se Mardeh, A., A. Ahmadi, K. Poustini and V. Mohammadi. 2006. Evaluation of drought resistance indices under various environmental conditions. Field Crops Research 98: 222 – 229

Slabbert, R., M. Spreeth and G. H. J. Krüger. 2004. Drought tolerance, traditional crops and biotechnology: breeding towards sustainable development. South African Journal of Botany 70: 116 – 123

Slafer, G. A., J. L. Araus and R. A. Richards. 1999. Physiological traits that increase the yield potential of wheat. Chapter 17, pp 379 – 414. *In*: E. H. Satorre and G. A. Slafer (Eds). Wheat: Ecology and physiology of yield determination. Haworth Press Inc., Binghamton

Sponchiado, B. N., J. W. White, J. A. Castillo and P. G. Jones. 1989. Root growth of four common bean cultivars in relation to drought tolerance in environments with contrasting soil types. Experimental Agriculture 25: 249 – 257

Sprent, J. I. 1972. The effects of water stress on nitrogen fixing root nodules. III. Effects of osmotically applied stress. New Phytologist 71: 451 – 460

Srinivasan, A., H. Takede and T. Senboku. 1996. Heat tolerance in food legumes as evaluated by cell membrane thermostability and chlorophyll fluorescence techniques. Euphytica 88: 35 – 45

Stanhill, G. 1986. Water use efficiency. Advances in Agronomy 39: 53 – 85

Streeter, J. G. 2003. Effects of drought on nitrogen fixation in soybean root nodules. Plant, Cell and Environment 26: 1199 – 1204

Subbarao, G. V. and C. Johansen. 2002. Transpiration efficiency: Avenues for genetic improvement. Chapter 43, pp 835 – 855. In: M. Pessarakli (Ed). Handbook of plant and crop physiology (Second Edition). Marcel Dekker, Inc, New York, Basel

Summerfield, R. J., F. R. Minchin, E. H. Roberts and P. Hadley. 1983. Cowpea. pp 249 – 280. *In:* Symposium on Potential Productivity of Field Crops Under Different Environments. International Rice Research Institute (IRRI), Los Baños Laguna, Manila, Philippines

Sutcliffe, J. F. 1968. Plants and water. Studies in Biology № 14 (Institute of Biology). Edward Arnold, London.

Tardieu, F. 1996. Drought perception by plants: do cells of droughted plants experience water stress? Plant Growth Regulation 20: 93 – 104

Tezara, W., V. J. Mitchell, S. D. Driscoll and D. W. Lawlor. 1999. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. Nature 401: 914 – 917

Tesfamariam, E. H., J. G. Annandale and J. M. Steyn. 2010. Water stress effects on winter canola growth and yield. Agronomy Journal 102: 658 – 666

Tewolde, H., A. K. Dobrenz, D. L. Robinson and V. Marcarian. 1990. Reproductive abscission and yield of irrigated and drought stressed cowpea. Journal of Agronomy and Crop Science 166: 191 – 199

The Royal Society. 2009. Reaping the benefits: science and the sustainable intensification of global agriculture. RS Policy document 11/09

Thiaw, S. And A. E. Hall. 2004. Comparison of selection for either leaf-electrolyte-leakage or pod set in enhancing heat tolerance and grain yield of cowpea. Field Crops Research 86: 239 – 253

Timko, M. P. and B. B. Singh. 2008. Cowpea, a multifunctional legume. Chapter 10, pp 227 – 258. P. H. Moore and R. Ming (Eds.). Genomics of tropical crop plants. Springer Verlag, Berlin

Tolk, J. A. and T. A. Howell. 2009. Transpiration and yield relationships of grain sorghum grown in a field environment. Agronomy Journal 101: 657 – 662

Tripathy, J. N., J. Zhang, S. Robin, Th. T. Nguyen and H. T. Nguyen. 2000. QTLs for cell-membrane stability mapped in rice (*Oryza sativa* L.) under drought stress. Theoretical and Applied Genetics 100: 1197 – 1202

Turk, K. J. and A. E. Hall. 1980a. Drought adaptation of cowpea. II. Influence of drought on plant water status, and relations with seed yield. Agronomy Journal 72: 421 – 427

Turk, K. J. and A. E. Hall. 1980b. Drought adaptation of cowpea. III. Influence of drought on plant growth and relations with seed yield. Agronomy Journal 72: 428 – 433

Turk, K. J., A. E. Hall and C. W. Asbell. 1980. Drought adaptation of cowpea. I. Influence of drought on seed yield. Agronomy Journal 72: 413 – 420

Turner, N. C., E.-D. Schulze and T. Gollan. 1984. The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. I. Species comparisons at high soil water contents. Oecologia 63: 338 – 342

Turner, N. C., J. E. Begg, H. M. Rawson, S. D. English and A. B. Hearn. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. III. Components of leaf water potential, leaf conductance, $^{14}CO_2$ photosynthesis, and adaptation to water deficits. Australian Journal of Plant Physiology 5: 179 – 194

UNEP (United Nations Environment Programme). 2007. Global Environmental Outlook Data Portal. http://geodata.grid.unep.ch. Accessed: 10 March 2010

van den Boogaard, R., M. De Boer, E. J. Veneklaas and H. Lambers. 1997. Growth and water-use efficiency of 10 *Triticum aestivum* cultivars at different water availability in relation to allocation of biomass. Plant, Cell and Environment 20: 200 – 210

van Ginkel, M., M. P. Reynolds, R. Trethowan and F. Hernandez. 2008. Complementing the breeder's eye with canopy temperature measurements. pp 134 – 135. *In*: M. P. Reynolds, J. Pietragalla and H. Braun (Eds.). International Symposium on Wheat Yield Potential: Challenges to International Wheat Improvement. Mexico, D. F., Mexico: CIMMYT

Villegas, D., N. Aparicio, R. Blanco and C. Royo. 2001. Biomass accumulation and main stem elongation of durum wheat grown under Mediterranean conditions. Annals of Botany 88: 617 – 627

von Caemmerer, S. and G. D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153: 376 – 387

Watanabe, I. 1998. Traits for drought tolerance in cowpea. JIRCAS Newsletter No. 14. Available on http://www.jircas.affrc.go.jp/kankoubutsu/news/newsletter/nl1998/no.14/watanabe.html

Watanabe, I., S. Hakoyama, T. Terao and B. B. Singh. 1997. Evaluation methods for drought tolerance in cowpea: 141 – 146; *In*: B. B. Singh, D. R. Mohan Raj, K. E. Dashiell and

L. E. N. Jackai (Eds). Advances in cowpea research. IITA and JIRCAS, Ibadan, Nigeria

Watanabe, I. and T. Terao. 1998. Drought tolerance of cowpea (*Vigna unguiculata* (L.) Walp.). II. Field trial in the dry season of Sudan savanna and dry matter production of potted plants under water stress. JIRCAS Journal 6: 29 – 37

Watt, B. K. and A. L. Merrill. 1975. Composition of foods. Agricultural Handbook No. 8. US Department of Agriculture. Washington DC

Westgate, M. E. and C. M. Peterson. 1993. Flower and pod development in water-deficient soybeans (*Glycine max* L. Merr.). Journal of Experimental Botany 44: 109 – 117

Wien, H. C. and R. J. Summerfield. 1980. Adaptation of cowpeas in West Africa: Effects of photoperiod and temperatureresponses in cultivars of diverse origin. pp 405 – 417. *In*: R. J. Summerfield and A. H. Bunting (Eds). Advances in legume science. HMSO, London

Wien, H. C. and R. J. Summerfield. 1984. Cowpea (*Vigna unguiculata* (L.) Walp.). pp 353 – 383. *In*: P. R. Goldworthy and N. M. Fisher (Eds). The physiology of tropical field crops. John Wiley and Sons,

Wienk, J. F. 1963. Photoperiodic effects in *Vigna unguiculata* (L.) Walp. Meded. Landbouwhogeschool Wageningen 63: 1 – 82

Zablotowicz, R. M., D. D. Focht and G. H. Cannell. 1981. Nodulation and N fixation of field-grown California cowpeas as influenced by well-irrigated and droughted conditions. Agronomy Journal 73: 9 – 12

Zegada-Lizarazu, W., L. Kanyomeka, Y. Izumi and M. Iijima. 2006. Pearl millet developed deep roots and changed sources by competition with intercropped cowpea in the semiarid environment of Northern Namibia. Plant Production Science 9: 355 – 363

APPENDIX

Experiment 1 *A*	bs	ww	wd	rew (ww)	rew (wd)
Ex Ukwala	4,55 **c**	13,73 **d**	1,39 **a**	14,10 **d**	13,59 **d**
UCR 328	8,99 **e**	14,42 **d**	9,13 **f**	14,73 **d**	13,79 **d**
UCR 1340	1,21 **a**	8,67 **bc**	6,36 **e**	8,96 **bc**	8,65 **bc**
IT 18	7,43 **d**	10,56 **c**	3,38 **d**	10,89 **c**	10,59 **c**
UCR 386	18,29 **f**	4,63 **a**	2,98 **c**	4,92 **a**	4,66 **a**
Lagreen	3,17 **b**	7,22 **b**	1,55 **b**	7,53 **b**	7,27 **b**
Mean	**7,27**	**9,87**	**4,13**	**10,19**	**9,76**

Experiment 2 *B*	bs	ww	wd	rew (ww)	rew (wd)
Ex Ukwala	7,20 **d**	5,65 **e**	1,94 **a**	6,13 **d**	5,95 **d**
UCR 328	8,23 **e**	7,48 **f**	4,31 **d**	7,97 **e**	7,63 **e**
UCR 1340	16,48 **f**	4,38 **c**	1,83 **a**	4,87 **b**	4,69 **b**
IT 18	5,91 **b**	8,35 **g**	5,80 **f**	8,86 **f**	8,59 **f**
UCR 386	20,28 **g**	3,65 **b**	3,15 **bc**	3,65 **a**	3,45 **a**
Lagreen	**n.m.**	11,60 **h**	6,85 **g**	12,13 **g**	11,89 **g**
Vita 7	5,44 **a**	8,50 **g**	5,16 **e**	5,65 **c**	5,43 **c**
TVu 12348	16,32 **f**	5,28 **d**	3,41 **c**	5,80 **c**	5,59 **c**
IFH 27-8	6,42 **c**	3,02 **a**	2,73 **b**	3,53 **a**	3,41 **a**
Mean	**9,59**	**6,44**	**3,91**	**6,51**	**6,29**

Experiment 3 *C*	bs	ww	wd	rew (ww)	rew (wd)
UCR 328	8,15 **c**	8,99 **c**	3,60 **bc**	9,83 **c**	10,75 **e**
UCR 1340	3,49 **a**	5,21 **a**	2,30 **a**	5,42 **a**	5,60 **a**
IT 18	13,95 **e**	6,85 **b**	2,278**a**	6,95 **b**	7,21 **c**
UCR 386	3,96 **a**	9,62 **d**	2,60 **a**	9,88 **c**	9,83 **d**
Lagreen	6,43 **b**	5,37 **a**	2,27 **a**	5,54 **a**	5,93 **a**
Vita 7	8,06 **c**	5,31 **a**	3,38 **b**	5,76 **a**	6,57 **b**
IFH 27-8	9,93 **d**	12,45 **e**	3,87 **c**	13,61 **d**	14,04 **f**
Mean	**7,71**	**7,69**	**2,90**	**8,14**	**8,56**

Table A1: Net photosynthetic rate, P_N (µmol m^{-2} s^{-1}) for experiment 1 (***A***) (N = 4), experiment 2 (***B***) (N = 6) and experiment 3 (***C***) (N = 5) of plants grown under well-watered (ww) and water deficit (wd) conditions. Same letters denote statistically similar values ($P \leq 0,05$, Duncan's Multiple Range Test, DMRT) within an experiment and column**.** bs: before stress; se: stress end, that is at maximum stress; rew: 4d after resumption of full irrigation (rewatering); n.m.: not measured

	Experiment 1: Transpiration rate, E (mmol m^{-2} s^{-1}) ***A***				
	ww (bs)	**ww (se)**	**wd (se)**	**ww (rew)**	**wd (rew)**
Ex Ukwala	0,87 **b**	6,17 **d**	0,29 **a**	6,12 **d**	6,01 **d**
UCR 328	1,81 **d**	4,89 **c**	1,87 **e**	5,26 **d**	4,95 **c**
UCR 1340	0,69 **a**	3,06 **b**	0,99 **d**	3,36 **b**	3,34 **b**
IT 18	1,11 **c**	3,99 **bc**	0,66 **c**	4,32 **c**	4,27 **c**
UCR 386	6,20 **e**	1,01 **a**	0,38 **b**	1,32 **a**	1,29 **a**
Lagreen	0,88 **b**	2,96 **ab**	0,37 **b**	3,27 **b**	3,26 **b**
Mean	**1,93**	**3,68**	**0,76**	**3,94**	**3,85**

	Experiment 2: Transpiration rate, E (mmol m^{-2} s^{-1}) ***B***				
	E (bs) ww	**E (se) ww**	**E (se) wd**	**E (rew) ww**	**E (rew) wd**
Ex Ukwala	3,24 **b**	2,29 **c**	0,61 **a**	2,86 **c**	2,81 **c**
UCR 328	4,09 **c**	2,96 **e**	2,08 **e**	3,42 **e**	3,33 **d**
UCR 1340	2,92 **b**	2,64 **d**	0,95 **b**	3,11 **cd**	3,01 **c**
IT 18	4,16 **c**	4,34 **f**	3,07 **f**	4,88 **f**	4,81 **e**
UCR 386	4,45 **c**	1,34 **a**	0,89**ab**	1,52 **a**	1,46 **a**
Lagreen	**n. m.**	5,90 **h**	3,00 **f**	6,33 **g**	6,28 **f**
Vita 7	1,90 **a**	4,91 **g**	3,85 **g**	3,04 **c**	2,93 **c**
TVu 12348	3,30 **b**	2,85 **de**	1,75 **d**	3,36 **de**	3,28 **d**
IFH 27-8	4,35 **c**	1,72 **b**	1,34 **c**	1,92 **b**	1,90 **b**
Mean	**3,16**	**3,22**	**1,93**	**3,38**	**3,31**

	Experiment 3: Transpiration rate, E (mmol m^{-2} s^{-1}) ***C***				
	ww (bs)	**ww (se)**	**ww (rew)**	**wd (se)**	**wd (rew)**
UCR 328	2,94 **a**	6,56 **f**	7,00 **d**	1,11 **ab**	8,03 **d**
UCR 1340	2,76 **a**	4,17 **c**	4,62 **a**	1,26 **b**	4,96 **a**
IT 18	6,71 **b**	5,68 **e**	5,86 **c**	1,16 **ab**	5,98 **b**
UCR 386	2,42 **a**	8,41 **g**	8,65 **e**	1,13 **ab**	8,91 **e**
Lagreen	2,60 **a**	3,61 **b**	4,74 **a**	1,05 **a**	5,15 **a**
Vita 7	2,55 **a**	3,37 **a**	5,19 **b**	1,94 **d**	5,88 **b**
IFH 27-8	3,09 **a**	5,51 **d**	5,90 **c**	1,67 **c**	7,45 **c**
Mean	3,29	5,33	5,99	1,33	6,62

Table A2: Transpiration rate (E) in mmol H_2O m^{-2} s^{-1} for Experiment 1 (***A***), N = 4; Experiment 2 (***B***), N = 6 and Experiment 3 (***C***), N = 5. Same letters within an experiment and column denote statistically similar values ($P \leq 0,05$) according to Duncan's Multiple Range Test. bs: before stress; se: stress end (maximum stress); rew: 4d after resumption of full irrigation; n. m.: not measured

A	**Experiment 1:** Stomatal conductance, g_s (mmol m^{-2} s^{-1})				
	ww (bs)	**ww (se)**	**wd (se)**	**ww (rew)**	**wd (rew)**
Ex Ukwala	57,7 **b**	391,9 **e**	8,7 **b**	362,3 **f**	367,7 **e**
UCR 328	97,8 e	137,4 d	21,0 d	141,7 e	158,7 d
UCR 1340	52,6 **a**	67,9 **b**	38,6 **f**	106,8 **c**	125,5 **c**
IT 18	74,0 d	114,6 c	22,3 e	121,8 d	131,9 c
UCR 386	253,1 **f**	21,8 **a**	12,3 **c**	61,3 **a**	78,1 **a**
Lagreen	70,2 **c**	65,1 **b**	7,4 **a**	74,0 **b**	86,8 **b**
Vita 7	-	-	-	-	-
TVu 12348	-	-	-	-	-
IFH 27-8	-	-	-	-	-
Mean	**100,9**	**133,1**	**18,4**	**144,6**	**158,1**

B	**Experiment 2:** Stomatal conductance, g_s (mmol m^{-2} s^{-1})				
	ww (bs)	**ww (se)**	**wd (se)**	**ww (rew)**	**wd (rew)**
Ex Ukwala	74,1 **cd**	43,7 **d**	7,6 **a**	55,0 **d**	76,7 **d**
UCR 328	92,3 **e**	77,3 **f**	15,6 **b**	92,6 **e**	108,6 **e**
UCR 1340	58,2 **bc**	15,9 **a**	9,4 **a**	30,5 **ab**	50,3 **a**
IT 18	117,3 f	75,1 f	64,7 f	91,1 e	109,9 e
UCR 386	89,7 **de**	19,9 **b**	20,6 **c**	33,0 **b**	54,0 **b**
Lagreen	**n. m.**	139,3 **g**	80,7 **g**	143,3 **f**	167,1 **f**
Vita 7	33,3 **a**	28,8 **c**	90,0 **h**	43,9 **c**	64,7 **c**
TVu 12348	42,0 **ab**	48,1 **e**	43,4 **e**	56,2 **d**	76,3 **d**
IFH 27-8	124,3 **f**	14,4 **a**	24,8 **d**	29,4 **a**	48,0 **a**
Mean	**70,1**	**51,4**	**39,6**	**63,9**	**83,9**

C	**Experiment 3:** Stomatal conductance, g_s (mmol m^{-2} s^{-1})				
	ww (bs)	**ww (se)**	**wd (se)**	**ww (rew)**	**wd (rew)**
UCR 328	28,50 **bc**	35,74 **f**	2,08 **a**	54,5 **e**	63,6 **e**
UCR 1340	42,55 **de**	15,26 **b**	5,26 **b**	25,1 **a**	38,7 **a**
IT 18	166,05 **f**	17,66 **d**	2,26 **a**	33,9 **c**	45,9 **c**
UCR 386	48,08 **e**	35,08 **f**	2,26 **a**	54,7 **e**	63,5 **e**
Lagreen	10,33 **a**	18,84 **c**	1,58 **a**	28,9 **b**	43,0 **b**
Vita 7	17,50 **ab**	13,88 **a**	1,32 **a**	27,7 **b**	42,8 **b**
IFH 27-8	31,18 **cd**	21,94 **e**	7,78 **c**	39,0 **d**	51,0 **d**
Mean	**49,17**	**22,67**	**3,22**	**37,7**	**49,8**

Table A3: Stomatal conductance (g_s) in mmol m^{-2} s^{-1} [N = 4 (experiment 1) or N = 6 (experiment 2) or N = 5 (experiment 3)] up to the end of water deficit (wd) stress (***A***) and after rewatering (***B***) for experiment 1 and 2. Same letters signify lack of difference within an experiment and column ($P \leq 0,05$) according to Duncan's Multiple Range Test. Abbreviations: bs: before stress; se: stress end (maximum wd stress); rew: four days after resumption of full irrigation; n. m.: not measured

Experiment 1 ***A***	**ww (bs)**	**ww (se)**	**wd (se)**	**ww (rew)**	**wd (rew)**
Ex Ukwala	5,22 **d**	2,22 **a**	4,87 **b**	2,30 **a**	2,25 **a**
UCR 328	4,96 **d**	2,95 **d**	4,87 **b**	2,80 **d**	2,79 **c**
UCR 1340	1,84 **a**	2,84 **cd**	6,44 **c**	2,67 **cd**	2,59 **bc**
IT 18	6,72 **e**	2,65 **bc**	5,11 **b**	2,52 **bc**	2,48 **b**
UCR 386	2,95 **b**	4,61 **e**	7,80 **d**	3,73 **e**	3,61 **d**
Lagreen	3,61 **c**	2,47 **b**	4,24 **a**	2,33 **ab**	2,25 **a**
Mean	**4,22**	**2,96**	**5,55**	**2,72**	**2,66**

Experiment 2 ***B***	**ww (bs)**	**ww (se)**	**wd (se)**	**ww (rew)**	**wd (rew)**
Ex Ukwala	2,23 **b**	2,46 **c**	3,21 **d**	2,15 **cd**	2,12 **cd**
UCR 328	2,03 **b**	2,52 **cd**	2,08 **bc**	2,33 **d**	2,29 **d**
UCR 1340	5,65 **f**	1,66 **a**	1,94 **bc**	1,57 **a**	1,56 **a**
IT 18	1,50 **a**	1,93 **ab**	1,91 **b**	1,82 **ab**	1,79 **ab**
UCR 386	4,57 **d**	2,78 **d**	3,57 **d**	2,40 **d**	2,36 **d**
Lagreen	**n. m.**	1,97 **b**	2,29 **c**	1,92 **bc**	1,90 **bc**
Vita 7	2,87 **c**	1,75 **ab**	1,41 **a**	1,86 **abc**	1,85 **abc**
TVu 12348	4,94 **e**	1,85 **ab**	1,97 **bc**	1,72 **ab**	1,71 **ab**
IFH 27-8	1,48 **a**	1,76 **ab**	2,09 **bc**	1,97 **bc**	1,93 **bc**
Mean	**2,81**	**2,08**	**2,27**	**1,97**	**1,94**

Experiment 3 ***C***	**ww (bs)**	**ww (se)**	**wd (se)**	**ww (rew)**	**wd (rew)**
UCR 328	3,69 **d**	1,37 **c**	3,24 **e**	1,41 **b**	1,34 **b**
UCR 1340	1,56 **a**	1,25 **b**	1,83 **ab**	1,18 **a**	1,13 **a**
IT 18	2,32 **bc**	1,21 **ab**	1,98 **bc**	1,19 **a**	1,21 **ab**
UCR 386	2,06 **ab**	1,15 **a**	2,31 **d**	1,14 **a**	1,11 **a**
Lagreen	2,88 **c**	1,49 **d**	2,16 **cd**	1,17 **a**	1,16 **a**
Vita 7	4,70 **e**	1,57 **d**	1,76 **a**	1,11 **a**	1,12 **a**
IFH 27-8	4,42 **e**	2,26 **e**	2,30 **d**	2,31 **c**	1,89 **c**
Mean	**3,09**	**1,47**	**2,23**	**1,36**	**1,28**

Table A4: Intrinsic transpiration efficiency (TE_i) in µmol CO_2 $mmol^{-1}$ H_2O just before the end of water deficit (wd) stress (maximum stress) for experiment 1 (***A***, N = 4), experiment 2 (***B***, N = 6) and experiment 3 (***C***, N = 5). Same letters signify lack of difference within an experiment and column ($P \leq 0,05$) according to Duncan's Multiple Range Test. bs: before stress; se: stress end (maximum wd stress); rew: 4d after resumption of full irrigation; n. m.: not measured

	Experiment 1: P_N/g_s			Experiment 2: P_N/g_s		
	ww (bs)	ww (se)	wd (se)	ww (bs)	ww (se)	wd (se)
Ex Ukwala	0,079 **d**	0,035 **a**	0,159 **a**	0,098 **b**	0,129 **c**	0,255 **e**
UCR 328	0,092 **e**	0,105 **bc**	0,436 **d**	0,093 **b**	0,097 **ab**	0,278 **e**
UCR 1340	0,023 **a**	0,128 **d**	0,165 **a**	0,284 **e**	0,276 **f**	0,202 **d**
IT 18	0,100 **f**	0,092 **b**	0,152 **a**	0,054 **a**	0,111 **b**	0,089 **ab**
UCR 386	0,072 **c**	0,213 **e**	0,243 **c**	0,227 **d**	0,158 **d**	0,153 **c**
Lagreen	0,045 **b**	0,112 **c**	0,212 **b**	**n. m.**	0,084 **a**	0,085 **ab**
Vita 7	-	-	-	0,164 **c**	0,182 **g**	0,095 **a**
TVu 12348	-	-	-	0,389 **f**	0,110 **b**	0,078 **a**
IFH 27-8	-	-	-	0,052 **a**	0,210 **e**	0,116 **b**
Mean	**0,069**	**0,114**	**0,228**	**0,151**	**0,167**	**0,144**

Table A5: The ratio P_N to g_s in µmol $mmol^{-1}$ just before the end of water deficit (wd) stress (maximum stress) for experiment 1 (N = 4) and 2 (N = 6). The same letters signify lack of difference within an experiment and column ($P \leq 0.05$) according to Duncan's Multiple Range Test. bs: before stress; se: stress end (maximum wd stress); n. m.: not measured

	Experiment 1: Water use (L $plant^{-1}$)			Experiment 2: Water use (L $plant^{-1}$)		
Genotype	**ww (bs)**	**ww (se)**	**wd (se)**	**ww (bs)**	**ww (se)**	**wd (se)**
Ex Ukwala	2,60	17,87 **a**	7,44 **d**	2,96 **e**	15,24 **f**	8,42 **h**
UCR 328	2,60	19,82 **b**	6,36 **a**	2,99 **f**	10,42 **bc**	7,28 **f**
UCR 1340	2,60	20,29 **b**	7,55 **b**	2,72 **d**	10,19 **b**	6,68 **c**
IT 18	2,60	18,38 **a**	7,39 **cd**	3,08 **g**	11,23 **d**	7,24 **e**
UCR 386	2,60	18,72 **a**	6,86 **b**	2,65 **c**	9,42 **a**	5,60 **a**
Lagreen	2,60	20,73 **b**	6,90 **bc**	2,63 **a**	11,50 **d**	6,92 **d**
Vita 7	-	-	-	3,08 **h**	11,98 **e**	8,18 **g**
TVu 12348	-	-	-	2,64 **b**	9,45 **a**	5,76 **b**
IFH 27-8	-	-	-	3,13 **i**	10,74 **c**	7,24 **e**
Mean	**2,60**	**19,30**	**7,08**	**2,88**	**11,13**	**7,04**

Table A6: Water use under well-watered (ww) and water deficit (wd) conditions for experiment 1 and experiment 2. Within each column, means followed by the same letter do not differ significantly at $P \leq 0,05$; n = 4 (experiment 1) and n = 6 (experiment 2) according to Duncan's Multiple Range Test (DMRT). bs: before stress; se: stress end (maximum wd stress)

	Experiment 1: Water use (L $plant^{-1}$)			Experiment 2: Water use (L $plant^{-1}$)		
	ww (bs)	ww (se)	wd (se)	ww (bs)	ww (se)	wd (se)
Ex Ukwala	2,60	7,60 ± 0,064 **a**	6,69 ± 0,026 **a**	2,96 ± 0,00 **e**	15,24 ± 0,003 **f**	8,42 ± 0,001 **h**
UCR 328	2,60	10,55 ± 0,293 **e**	7,36 ± 0,094 **cd**	2,99 ± 0,00 **f**	10,42 ± 0,001 **bc**	7,28 ± 0,001 **f**
UCR 1340	2,60	10,02 ± 0,068 **d**	7,55 ± 0,136 **d**	2,72 ± 0,00 **d**	10,19 ± 0,002 **b**	6,68 ± 0,001 **c**
IT 18	2,60	8,10 ± 0,277 **ab**	7,39 ± 0,182 **cd**	3,08 ± 0,00 **g**	11,23 ± 0,399 **d**	7,24 ± 0,001 **e**
UCR 386	2,60	8,45 ± 0,108 **bc**	6,86 ± 0,041 **ab**	2,65 ± 0,00 **c**	9,42 ± 0,000 **a**	5,60 ± 0,001 **a**
Lagreen	2,60	8,70 ± 0,047 **c**	7,10 ± 0,087 **bc**	2,63 ± 0,00 **a**	11,50 ± 0,004 **d**	6,92 ± 0,002 **d**
Vita 7	-	-	-	3,08 ± 0,00 **h**	11,98 ± 0,000 **e**	8,18 ± 0,003 **g**
TVu 12348	-	-	-	2,64 ± 0,00 **b**	9,45 ± 0,002 **a**	5,76 ± 0,002 **b**
IFH 27-8	-	-	-	3,13 ± 0,00 **i**	10,74 ± 0,001 **c**	7,24 ± 0,005 **e**
Mean	**2,60**	**8,90 ± 0,227**	**7,16 ± 0,075**	**2,88 ± 0,027**	**11,13 ± 0,233**	**7,04 ± 0,123**

Table A7: Water use (means ± standard error) under well-watered (ww) and water deficit (wd) conditions for experiment 1 and 2. Within each column, means followed by the same letter do not differ significantly at $P \leq 0,05$; N = 4 (experiment 1) and N = 6 (experiment 2) according to Duncan's Multiple Range Test (DMRT). bs: before stress; se: stress end (maximum wd stress)

	Exp 1: RGR (mg g^{-1} day^{-1})		**Exp 2:** RGR (mg g^{-1} day^{-1})	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	417 **a**	167 **ab**	61 **a**	52 **bc**
UCR 328	717 **b**	207 **b**	75 **ab**	6 **a**
UCR 1340	777 **b**	218 **b**	163 **d**	10 **ab**
IT 18	423 **a**	144 **a**	153 **cd**	12 **ab**
UCR 386	656 **b**	188 **ab**	99 **abc**	27 **abc**
Lagreen	656 **b**	189 **ab**	242 **e**	66 **cd**
Vita 7	-	-	113 **abcd**	44 **abc**
TVu 12348	-	-	84 **ab**	98 **d**
IFH 27-8	-	-	128 **bcd**	68 **cd**
Mean	**607**	**185** (31)	**124**	**42** (34)

Table A8: Relative growth rate (RGR) for Experiments 1 and 2 under well-watered (ww) and water deficit (wd) conditions. The numbers in brackets in the mean row show the relative value (in %) of the wd treatment compared to the ww treatment. Same letters signify lack of difference among genotypes within an experiment and column ($P \leq 0,05$) according to Duncan's Multiple Range Test.

	Exp 1: NAR (g m^{-2} d^{-1})			**Exp 2:** NAR (g m^{-2} d^{-1})		
	bs	**ww (se)**	**wd (se)**	**bs**	**ww (se)**	**wd (se)**
Ex Ukwala	1,48 **a**	2,86 **a**	2,26 **ab**	1,43 **c**	1,55 **a**	1,28 **abc**
UCR 328	1,63 **a**	4,00 **d**	2,76 **cd**	1,38 **bc**	2,49 **ab**	0,32 **a**
UCR 1340	1,49 **a**	3,08 **ab**	2,51 **bc**	1,19 **abc**	2,57 **bc**	0,42 **a**
IT 18	1,53 **a**	3,55 **c**	2,97 **d**	1,08 **a**	3,41 **c**	0,74 **ab**
UCR 386	1,61 **a**	3,29 **bc**	2,24 **a**	1,25 **abc**	1,98 **ab**	0,86 **ab**
Lagreen	1,62 **a**	3,51 **c**	2,54 **c**	1,01 **a**	2,25 **ab**	1,40 **abc**
Vita 7	-	-	-	1,16 **abc**	1,78 **ab**	1,12 **ab**
TVu 12348	-	-	-	1,11 **ab**	1,49 **a**	1,91 **bc**
IFH 27-8	-	-	-	1,11 **ab**	2,24 **ab**	2,56 **c**
Mean	**1,56**	**3,38**	**2,55** (75)	**1,19**	**2,19**	**1,18** (54)

Table A9: Net assimilation rate (NAR) for Experiment 1 to 3 under well-watered (ww) and water deficit (wd) conditions. The numbers in brackets in the mean row show the relative value (%) of the wd treatment compared to the ww treatment.. Same letters signify lack of difference among genotypes within an experiment and column ($P \leq 0,05$) according to Duncan's Multiple Range Test.

	Experiment 1			**Experiment 2**		
	ww (bs)	**ww (se)**	**wd (se)**	**ww (bs)**	**ww (se)**	**wd (se)**
Ex Ukwala	74,4 **d**	262,7 **b**	195,3 **c**	113,6 **d**	276,5 **d**	230,2 **c**
UCR 328	18,1 **a**	198,3 **a**	133,0 **a**	39,7 **ab**	152,8 **ab**	47,8 **a**
UCR 1340	31,0 **b**	317,0 **c**	220,3 **d**	27,8 **a**	188,2 **bc**	50,7 **a**
IT 18	41,3 **c**	202,3 **a**	159,7 **b**	54,4 **bc**	180,7 **bc**	47,3 **a**
UCR 386	29,5 **b**	216,0 **a**	155,0 **b**	35,2 **a**	108,5 **a**	69,7 **a**
Lagreen	112,0 **e**	240,0 **ab**	198,7 **c**	68,8 **c**	230,2 **cd**	133,0 **b**
Vita 7	-	-	-	56,9 **bc**	174,5 **b**	126,0 **b**
TVu 12348	-	-	-	44,0 **ab**	141,7 **ab**	135,2 **b**
IFH 27-8	-	-	-	58,5 **bc**	146,2 **ab**	81,1 **a**
Mean	**51,04**	**239,4**	**177,0**	**55,4**	**177,7**	**102,3**

Table A10: Main stem length [N = 4 (experiment 1) or N = 6 (experiment 2)] as affected by treatment (ww and wd) in experiment 1 and 2. The same letters signify lack of difference in the appropriate experiment and column ($P \leq 0,05$).

	Experiment 1: Leaf mass ratio			**Experiment 2:** Leaf mass ratio		
	ww (bs)	**ww (se)**	**wd (se) wd**	**ww (bs)**	**ww (se)**	**wd (se)**
Ex Ukwala	0,615 **b**	0,486 **b**	0,445 **a**	0,544 **b**	0,454 **bc**	0,435 **b**
UCR 328	0,709 **c**	0,534 **c**	0,482 **b**	0,624 **d**	0,481 **cd**	0,443 **b**
UCR 1340	0,684 **c**	0,503 **b**	0,557 **d**	0,675 **e**	0,541 **e**	0,529 **bc**
IT 18	0,630 **b**	0,457 **a**	0,462 **ab**	0,567 **bc**	0,434 **b**	0,458 **bc**
UCR 386	0,695 **c**	0,567 **d**	0,554 **d**	0,637 **d**	0,552 **e**	0,516 **bc**
Lagreen	0,563 **a**	0,505 **b**	0,510 **c**	0,499 **a**	0,528 **e**	0,551 **c**
Vita 7	-	-	-	0,542 **b**	0,514 **de**	0,468 **bc**
TVu 12348	-	-	-	0,639 **d**	0,604 **f**	0,491 **bc**
IFH 27-8	-	-	-	0,580 **c**	0,397 **a**	0,341 **a**
Mean	0,649	0,509	0,502	0,590	0,501	0,470

Table A11: Leaf mass ratio (LMR) under well-watered (ww) and water deficit (wd) conditions for experiment 1 (N = 4) and experiment 2 (N = 6). The same letters signify lack of difference in the appropriate experiment and column (P ≤ 0,05). bs: before stress; se: stress end (maximum wd stress)

	Experiment 1:		**Experiment 2:**	
	ww	**wd**	**ww**	**wd**
Ex Ukwala	1,9 ± 0,27 **c**	4,1 ± 0,07 **d**	2,5 ± 0,22 **e**	5,0 ± 0,23 **c**
UCR 328	1,1 ± 0,13 **a**	2,8 ± 0,12 **a**	1,8 ± 0,12 **abc**	3,1 ± 0,13 **a**
UCR 1340	1,7 ± 0,05 **bc**	3,3 ± 0,09 **bc**	2,2 ± 0,10 **cde**	4,1 ± 0,34 **b**
IT 18	1,7 ± 0,13 **bc**	3,6 ± 0,09 **c**	2,3 ± 0,16 **de**	4,0 ± 0,04 **b**
UCR 386	1,9 ± 0,15 **c**	3,4 ± 0,18 **c**	2,3 ± 0,09 **de**	4,3 ± 0,31 **b**
Lagreen	1,2 ± 0,23 **ab**	3,0 ± 0,15 **ab**	1,9 ± 0,22 **bcd**	3,3 ± 0,29 **a**
Vita 7	-	-	1,4 ± 0,14 **a**	3,3 ± 0,10 **a**
TVu 12348	-	-	1,3 ± 0,13 **a**	2,7 ± 0,24 **a**
IFH 27-8	-	-	1,5 ± 0,06 **ab**	2,6 ± 0,17 **a**
Mean	**1,6 ± 0,09**	**3,3** ± 0,10	**1,9** ± 0,07	**3,6** ± 0,12

Table A12: Leaf-air temperature differential, ΔT, (°C) (means ± standard error) of well-watered (ww) and water deficit (wd) treatments for experiment 1 (N = 4 for each treatment) and experiment 2 (N = 6 for each treatment). The same letters signify similarity among genotypes in the appropriate experiment and column (P ≤ 0,05). Leaf-air temperature differential was determined as follows: T_{leaf} minus T_{air}.

A	**E**	**P_N**	**g_s**	**P_N/g_s**	**TE_i**
E	-				
P_N	0.952**	-			
g_s	0.820**	0.685**	-		
P_N/g_s	-0.864**	-0.728**	-0.818**	-	
TE_i	-0.733**	-0.585**	-0.571**	0.923**	-
ETE	n. s.	n. s.	-0.473*	n. s.	n. s.

B	**E**	**P_N**	**g_s**	**P_N/g_s**	**TE_i**
E	-				
P_N	0,971**	-			
g_s	0,519**	0,659**	-		
P_N/g_s	0,788**	0,712**	n. s.	-	
TE_i	n. s.	n. s.	n. s.	n. s.	-
ETE	n. s.	n. s.	-0,543**	0,683**	-0,578**

Table A13: Linear correlations in experiment 1 among gas exchange parameters and ETE under well-watered (***A***) and water deficit (***B***) conditions (**: P ≤ 0.01 and *: P ≤ 0.05). n. s.: not significant

A	LA	SLA	LMR	SMLR	SMR	RGR	NAR
E	n. s.	n. s.	-0.458*	-0,416*	n. s.	n. s.	n. s.
P_N	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.
g_s	n. s.	0.518*	n. s.	-0.410*	n. s.	-0.517**	n. s.
P_N/g_s	n. s.	-0.457*	0.675**	0.641**	0.575**	0.459*	n. s.
TE_i	n. s.	-0.444*	0.702**	0.770**	0.721**	n. s.	n. s.
ETE	n. s.	-0.526**	n. s.	n. s.	n. s.	0.741**	0.565**

B	LA	SLA	LMR	SMLR	SMR	RGR	NAR
E	n. s.	n. s.	-0.458*	-0,416*	n. s.	n. s.	n. s.
P_N	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.
g_s	n. s.	0.518*	n. s.	-0.410*	n. s.	-0.517**	n. s.
P_N/g_s	n. s.	-0.457*	0.675**	0.641**	0.575**	0.459*	n. s.
TE_i	n. s.	-0.444*	0.702**	0.770**	0.721**	n. s.	n. s.
ETE	n. s.	-0.526**	n. s.	n. s.	n. s.	0.741**	0.565**

Table A14: Linear correlations in experiment 1 among gas exchange, evapotranspiration efficiency, biomass partitioning and growth under well-watered (***A***) and water deficit (***B***)conditions (**: $P \leq 0.01$ and *: $P \leq 0.05$). n. s.: not significant

A	LA	SLA	LMR	SMLR	SMR	RGR	NAR
E	n. s.	n. s.	0,205*	-0,387**	n. s.	0,483**	n. s.
P_N	n. s.	n. s.	0,563**	-0,348**	n. s.	0,413**	n. s.
g_s	n. s.	n. s.	0,230*	-0,287*	n. s.	0.416*	n. s.
TE_i	n. s.	n. s.	0,543**	-0,299*	n. s.	-0,355**	n. s.
ETE	0,496**	-0,651**	n. s.	0,341**	n. s.	0,387**	0,520**

B	LA	SLA	LMR	SMLR	SMR	RGR	NAR
E	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.
P_N	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.
g_s	n. s.	n. s.	n. s.	-0,325*	n. s.	n. s.	n. s.
TE_i	0,307*	n. s.	n. s.	n. s.	n. s.	n. s.	n. s.
ETE	0,755**	n. s.	n. s.	0,296*	n. s.	0,738**	0,464**

Table A15: Linear correlations in experiment 2 among gas exchange, evapotranspiration efficiency, biomass partitioning and growth under well-watered (***A***) and water deficit (***B***) conditions (**: $P \leq 0.01$ and *: $P \leq 0.05$). n. s.: not significant

	Exp 1		Exp 2		Exp 3
	DM_{anth}	**DM_{mat}**	**DM_{anth}**	**DM_{mat}**	**DM_{anth}**
LA (ww)	0,623**	n. s.	0,516**	0,285*	0,896**
SLA (ww)	-0,499*	0,621**	-0,423**	n. s.	0,369*
LA (wd)	0,436*	0,719**	0,876**	0,305*	0,403*
SLA (wd)	n. s.	0,614**	n. s.	n. s.	n. s.

Table A16: Linear correlations between leaf area (LA) and specific lea area (SLA) on the one side and DM at anthesis (DM_{anth}) and at maturity (DM_{mat}) at the other side under ww and wd conditions in experiments 1 to 3. * shows significant correlations at the 0,05 probability level and ** at the 0,01 level. n. s.: not significant

Ex1,ww	P_N	E	g_s	TE_i	P_N/g_s	Y	HI	ΔT	WU_{anth}
LSS	n.s.	0,613**	0,762**	-0,705**	-0,766**	0,714**	-0,628**	n.s.	n.s.
Ex1,wd	P_N	E	g_s	TE_i	P_N/g_s	Y	HI	ΔT	WU_{anth}
LSS	-0,667**	-0,666**	n.s.	n.s.	-0,839**	-0,648**	-0,494*	0,633**	0,658**
Ex2,ww	P_N	E	g_s	TE_i	P_N/g_s	Y	HI	ΔT	WU_{anth}
LSS	n.s.	n.s.	n.s.	n.s.	n.s.	-0,269*	-0,338*	0,385**	0,630**
Ex2,wd	P_N	E	g_s	TE_i	P_N/g_s	Y	HI	ΔT	WU_{anth}
LSS	n.s.	n.s.	n.s.	n.s.	n.s.	-0,465**	-0,452**	0,582**	0,570**
Ex3,ww	P_N	E	g_s	TE_i	P_N/g_s	Y	HI	ΔT	WU_{anth}
LSS	-0,340*	-0,470**	-0,495**	n.s.	n.s.	N/A	N/A	n.s.	n.s.
Ex3,wd	P_N	E	g_s	TE_i	P_N/g_s	Y	HI	ΔT	WU_{anth}
LSS	-0,416**	n.s.	n.s.	-0,878**	n.s.	N/A	N/A	n.s.	0,632**

Table A17: Linear correlations in experiment 1 (Ex1), experiment 2 (Ex2) and experiment 3 (Ex3) between leaf shedding (LSS) and some traits of cowpea under well-watered (ww) and water deficit (wd) conditions. *P ≤ 0,05 and ** P ≤ 0,01; N/A: not applicable; n.s.: not significant

	P_N/g_s	P_N/C_i	ETE	SLA	SMLR	RWC
ΔT	-0,632**	-0,515**	**-0,469***	0,409*	-0,484*	-0,594**
	Pod№	PodYield	Seed№	Yield	SGM	HI
ΔT	-0,587**	-0,723**	-0,513*	-0,759**	-0,785** **-0,459***	-0,602** **-0,496***
	ShOutturn	WUE_{mat}	LSS	$Time_{Anth}$	$Time_{Mat}$	Anth-to-Mat
ΔT	-0,544**	-0,724** **-0,463***	0,639**	0,638**	0,551** **0,496***	-0,685**
	ΔP_N	ΔE	$\Delta P_N/g_s$			
ΔT	0,507*	0,585**	0,567**			

Table A18: Linear correlations in experiment 1 between ΔT and other traits under well-watered and water deficit conditions (**: P ≤ 0.01 and *: P ≤ 0.05). Values in **bold** indicate correlations under ww conditions and all other values indicate correlation coefficients under wd conditions. $Time_{Anth}$: time to anthesis; $Time_{Mat}$: time to maturity; Anth-to-Mat: time from anthesis to maturity; ShOutturn: shelling outturn; WUE_{mat}: water-use efficiency at maturity determined as seed yield/total water used; LSS: leaf shedding score

Experiment 2	P_N/g_s	ETE	SMLR	RWC	CMS
ΔT	0,297*	-0,291*	-0,321*	-0,474**	-0,531**
Experiment 2	PodYield	Yield	SGM	HI	WUE_{mat}
ΔT	-0,283*	-0,369**	-0,325*	-0,315*	-0,424**
Experiment 2	$Time_{Anth}$	Anth-to-Mat	Δg_s	LSS	TE_i
ΔT	0,800** **0,515****	-0,364*	-0,539**	0,530** **0,376****	0,454** **0,346***
Experiment 3	ETE	RWC			
ΔT	-0,482**	-0,488**			

Table A19: Linear correlations in experiment 2 and experiment 3 between ΔT and all other traits under well-watered and water deficit conditions (**: $P \leq 0.01$ and *: $P \leq 0.05$). Values in **bold** indicate correlations under ww conditions and all other values indicate correlation coefficients under wd conditions. $Time_{Anth}$: time to anthesis; TE_i: intrinsic transpiration efficiency (P_N/E); Anth-to-Mat: time from anthesis to maturity; WUE_{mat}: water-use efficiency at maturity determined as seed yield/total water used; LSS: leaf shedding score

A	PodNum	PodY	SeedNum	Y	SGM	HI	ShOut
P_n	-0,752**	-0,371	-0,612**	-0,255	0,457*	-0,097	0,414*
g_s	-0,919**	-0,871**	-0,863**	-0,807**	-0,106	-0,706**	0,076
TE_i	0,517*	0,383	0,488*	0,267	-0,190	0,135	-0,514*
$P_n g_s$	0,757**	0,586**	0,674**	0,469*	-0,148	0,317	-0,461*
ETE	0,379	0,419*	0,197	0,413*	0,452*	0,314	0,154
DM_{anth}	0,421*	0,440*	0,202	0,453*	0,466*	0,341	0,222
LA	0,231	-0,026	0,020	-0,087	-0,191	-0,226	-0,326
SLA	-0,356	-0,587**	-0,305	-0,611**	-0,672**	-0,615**	-0,343
SMLR	0,261	0,411*	0,285	0,378	0,314	0,319	-0,052
RWC	-0,413*	-0,052	-0,382	0,093	0,715**	0,257	0,764**
DM_{mat}	-0,474*	-0,736**	-0,571**	-0,760**	-0,493*	-0,867**	-0,432*
ETE_{mat}	-0,382	-0,351	-0,509*	-0,314	0,216	-0,435*	0,028
WUE	0,559**	0,903**	0,632**	0,951**	0,671**	0,948**	0,503*
Nodes	-0,692**	-0,414*	-0,543**	-0,359	0,229	-0,247	0,197
NoBra	-0,575**	-0,741**	-0,645**	-0,724**	-0,305	-0,676**	-0,154
LSS	-0,645**	-0,756**	-0,637**	-0,714**	-0,335	-0,628**	0,009
$Time_{anth}$	-0,617**	-0,898**	-0,642**	-0,894**	-0,405	-0,872**	-0,176
$Time_{mat}$	-0,610**	-0,883**	-0,721**	-0,909**	-0,476*	-0,957**	-0,396
$T_{anth-mat}$	0,660**	0,882**	0,633**	0,861**	0,379	0,806**	0,103
ΔT	-0,022	-0,257	0,031	-0,333	-0,628	-0,408	-0,513*
WU_{anth}	0,440*	0,448*	0,237	0,471*	0,411*	0,367	0,251
WU_{mat}	-0,315	-0,670**	-0,364	-0,726**	-0,757**	-0,803**	-0,565**

B	PodNum	PodY	SeedNum	Y	SGM	HI	ShOut
P_n	0,226	0,553**	0,357	0,612**	0,602**	0,648**	0,509*
g_s	0,271	0,414*	0,520**	0,434*	0,193	0,578**	0,269
TE_i	0,397	0,246	0,422*	0,126	-0,170	-0,096	-0,631**
P_n/g_s	0,163	0,437*	0,087	0,486*	0,661**	0,357	0,397
ETE	-0,228	-0,038	-0,359	0,036	0,420*	-0,013	0,282
DM_{anth}	-0,532**	-0,470*	-0,532**	-0,401	-0,193	-0,302	0,264
LA	-0,390	-0,584**	-0,529**	-0,599**	-0,471*	-0,791**	-0,352
SLA	-0,653**	-0,776**	-0,785**	-0,785**	-0,508*	-0,863**	-0,480*
SMLR	0,320	0,563**	0,303	0,556**	0,580**	0,416*	0,115
RWC	0,084	0,321	-0,027	0,398	0,662**	0,362	0,538**
DM_{mat}	-0,073	-0,326	-0,261	-0,412*	-0,428*	-0,748**	-0,629**
WU_{mat}	-0,281	-0,570**	-0,433*	-0,646**	-0,537**	-0,868**	-0,731**
ETE_{mat}	0,245	0,208	0,093	0,168	0,030	-0,168	-0,071
WUE	0,667**	0,907**	0,741**	0,949**	0,788**	0,964**	0,710**
Nodes	-0,264	-0,139	-0,073	-0,095	-0,017	0,125	0,015
NoBra	-0,622**	-0,602**	-0,614**	-0,551**	-0,361	-0,368	0,127
LSS	-0,436*	-0,651**	-0,400	-0,648**	-0,614**	-0,494*	-0,245
$Time_{anth}$	-0,551**	-0,819**	-0,514*	-0,838**	-0,858**	-0,711**	-0,640**
$Time_{mat}$	-0,659**	-0,841**	-0,716**	-0,865**	-0,735**	-0,935**	-0,612**
$T_{anth-mat}$	0,628**	0,824**	0,545*	0,829**	0,843**	0,609**	0,364
ΔT	-0,578**	-0,732**	-0,506*	-0,780**	-0,747**	-0,631**	-0,587**
DM_{susin}	-0,411*	-0,447*	-0,288	-0,443*	-0,473*	-0,163	-0,049
Y_{susind}	-0,829**	-0,902**	-0,791**	-0,900**	-0,741**	-0,729**	-0,338

Table A20: Linear correlations in experiment 1 between selected traits and yield/yield components under well-watered **(*A*)** and water deficit **(*B*)** conditions**.** * denotes significant correlations at the 0,05 probability level and ** at the 0,01 level. $Time_{Anth}$: time to anthesis; TE_i: intrinsic transpiration efficiency (P_N/E); Anth-to-Mat: time from anthesis to maturity; WUE_{mat}: water-use efficiency at maturity determined as seed yield/total water used; LSS: leaf shedding score; Nodes: total number of leaf nodes on the main stem; NoBra: number of branches; DM_{susin}: biomass stress susceptibility index; Y_{susin}: yield stress susceptibility index; PodNum: number of pods $plant^{-1}$; PodY: pod yield $plant^{-1}$; SeedNum: number of seeds $plant^{-1}$; Y: seed yield $plant^{-1}$

A	**PodNum**	**PodY**	**SeedNum**	**Y**	**SGM**	**HI**	**ShOut**
P_n	-0,367**	0,118	-0,068	0,117	0,084	0,002	-0,125
g_s	-0,147	0,345*	0,142	0,350**	0,408**	0,267	0,219
TE_i	0,148	0,064	0,098	0,088	-0,001	0,051	-0,011
P_ng_s	-0,042	-0,309*	-0,188	-0,329*	-0,433**	-0,339*	-0,345*
ETE	0,394**	0,345*	0,346*	0,366**	0,346*	0,414**	0,381**
DM_{anth}	0,103	0,128	0,096	0,142	0,063	0,166	0,023
LA	-0,432**	-0,508**	-0,465**	-0,491**	-0,394**	-0,466**	-0,381**
SLA	-0,384**	-0,499**	-0,462**	-0,480**	-0,341*	-0,406**	-0,325*
SMLR	0,612**	0,422**	0,485**	0,451**	0,302*	0,495**	0,366**
RWC	0,041	0,290*	0,070	0,363**	0,474**	0,481**	0,274*
DM_{mat}	-0,560**	-0,507**	-0,475**	-0,499**	-0,752**	-0,701**	-0,809**
ETE_{mat}	-0,210	-0,024	-0,128	0,027	-0,231	-0,169	-0,385**
WUE	0,748**	0,920**	0,800**	0,957**	0,857**	0,972**	0,810**
Nodes	-0,664**	-0,659**	-0,713**	-0,623**	-0,487**	-0,568**	-0,617**
NoBra	-0,224	-0,045	-0,196	0,032	0,140	0,097	-0,052
LSS	-0,382**	-0,257	-0,256	-0,269*	-0,401**	-0,338**	-0,459**
$Time_{anth}$	0,110	0,132	0,325*	0,013	-0,434**	-0,319*	-0,365*
$Time_{mat}$	-0,754**	-0,762**	-0,738**	-0,769**	-0,890**	-0,839**	-0,973**
$T_{anth-mat}$	-0,147	0,005	-0,124	-0,058	0,026	0,010	-0,221
ΔT	0,130	0,121	0,215	0,107	-0,140	0,002	-0,046
WU_{anth}	-0,635**	-0,509**	-0,570**	-0,497**	-0,599**	-0,545**	-0,753**
WU_{mat}	-0,571**	-0,586**	-0,491**	-0,599**	-0,813**	-0,776**	-0,804**

B	**PoNum**	**PoY**	**SNum**	**SeY**	**SGM**	**HI**	**ShOut**
P_n	0,088	0,363**	0,314*	0,343*	0,163	0,109	0,131
g_s	-0,181	0,049	0,078	0,044	-0,165	-0,158	-0,137
TE_i	0,115	-0,075	-0,019	-0,128	-0,176	-0,304*	-0,137
P_ng_s	-0,007	-0,060	-0,199	-0,066	0,065	0,075	-0,091
ETE	0,020	-0,124	0,076	-0,123	-0,132	-0,185	0,012
DM_{anth}	-0,202	-0,274*	-0,170	-0,247	-0,273*	-0,296*	-0,257
LA	-0,315*	-0,395**	-0,270*	-0,408**	-0,515*	-0,473**	-0,469**
SLA	-0,092	-0,172	-0,192	-0,180	-0,145	-0,123	-0,165
SMLR	0,489**	0,249	0,211	0,261	0,481**	0,396**	0,398**
RWC	0,249	0,421**	0,301*	0,472**	0,406**	0,354**	0,267
CMS	0,499**	0,513**	0,509**	0,536**	0,589**	0,549**	0,578**
DM_{mat}	-0,322*	-0,326*	-0,325*	-0,349**	-0,656**	-0,675**	-0,745**
ETE_{mat}	0,072	-0,109	-0,150	-0,082	-0,239	-0,261	-0,398**
WUE	0,724**	0,797**	0,659**	0,847**	0,811**	0,911**	0,684**
Nodes	-0,551**	-0,557**	-0,488**	-0,537**	-0,693**	-0,599**	-0,722**
NoBra	-0,020	0,073	0,060	0,111	0,111	0,000	0,063
LSS	-0,550**	-0,458**	-0,501**	-0,465**	-0,493**	-0,452**	-0,552**
$Time_{anth}$	-0,132	-0,276	-0,186	-0,423**	-0,546**	-0,388*	-0,702**
$Time_{mat}$	-0,666**	-0,583**	-0,576**	-0,601**	-0,857**	-0,745**	-0,928**
$T_{anth-mat}$	-0,078	0,249	0,407**	0,219	-0,165	-0,160	-0,063
ΔT	-0,193	-0,379	-0,347	-0,453	-0,470	-0,434	-0,447**
DM_{susin}	-0,075	-0,267	-0,285*	-0,279*	0,073	0,075	0,140
Y_{susind}	0,162	-0,075	-0,059	-0,107	0,247	0,042	0,350**
WU_{anth}	-0,486**	-0,318*	-0,543**	-0,251	-0,317*	-0,210	-0,610**
WU_{mat}	-0,336*	-0,142	0,136	-0,181	-0,489**	-0,571**	-0,512**

Table A21: Linear correlations in experiment 2 between selected traits and yield/yield components under well-watered **(*A*)** and water deficit **(*B*)** conditions**.** * denotes significant correlations at the 0,05 probability level and ** at the 0,01 level. $Time_{Anth}$: time to anthesis; TE_i: intrinsic transpiration efficiency (P_N/E); Anth-to-Mat: time from anthesis to maturity; WUE_{mat}: water-use efficiency at maturity determined as seed yield/total water used; LSS: leaf shedding score; Nodes: total number of leaf nodes on the main stem; NoBra: number of branches; DM_{susin}: biomass stress susceptibility index; Y_{susin}: yield stress susceptibility index; CMS: cell membrane stability index

	Experiment 1		Experiment 2	
	ww	wd	ww	wd
Ex Ukwala	185,54 ± 14,00 **c**	131,67 ± 6,89 **d**	39,52 ± 1,71 **d**	30,35 ± 2,31 **c**
UCR 328	107,11 ± 7,93 **a**	95,69 ± 3,87 **b**	21,90 ± 0,80 **abc**	14,57 ± 0,93 **b**
UCR 1340	123,82 ± 5,20 **ab**	93,99 ± 1,62 **b**	25,54 ± 2,75 **c**	8,09 ± 2,27 **a**
IT 18	105,00 ± 1,13 **a**	75,04 ± 2,18 **a**	23,35 ± 1,98 **bc**	11,67 ± 0,44 **ab**
UCR 386	136,85 ± 1,58 **b**	150,31 ± 1,21 **e**	25,14 ± 2,22 **c**	24,69 ± 4,18 **c**
Lagreen	120,28 ± 8,96 **ab**	111,33 ± 4,99 **c**	26,31 ± 1,94 **c**	24,32 ± 1,37 **c**
Vita 7	-	-	45,82 ± 2,20 **e**	39,85 ± 1,85 **d**
TVu 12348	-	-	17,00 ± 1,19 **a**	15,49 ± 1,01 **b**
IFH 27-8	-	-	17,76 ± 1,21 **ab**	14,91 ± 1,15 **b**
Mean	**129,77 ± 6,33**	**109,67 ± 5,43**	**26,92 ± 1,37**	**20,44 ± 1,46**

Table A22: Shoot biomass (DM) at maturity (means ± standard error) under well-watered (ww) and water deficit (wd) conditions for experiment 1 and 2. Within each column, means followed by the same letter do not differ significantly ($P < 0.05$).

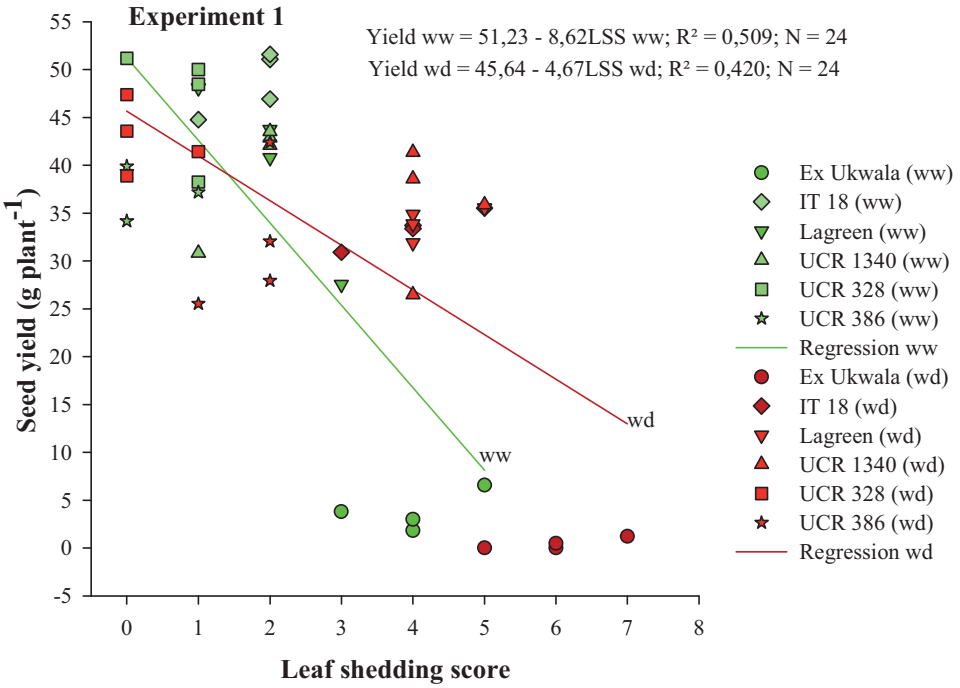

Fig A1: Regression analysis of leaf shedding score (LSS) against seed yield under well-watered (ww) and water deficit (wd) conditions in experiment 1

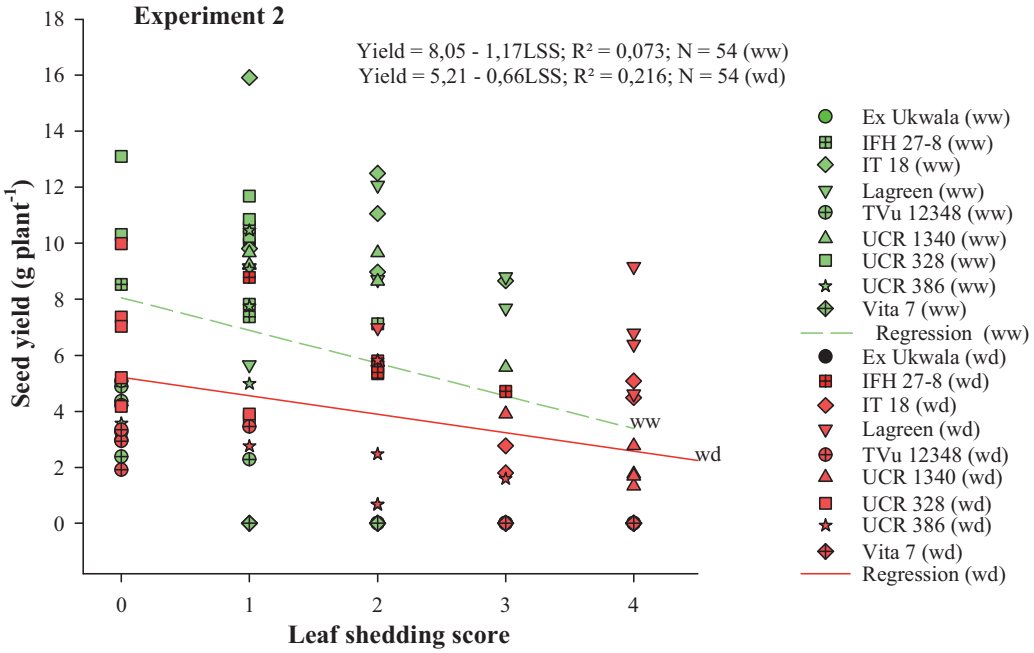

Fig A2: Regression analysis of leaf shedding score (LSS) against seed yield under well-watered (ww) and water deficit (wd) conditions in experiment 2

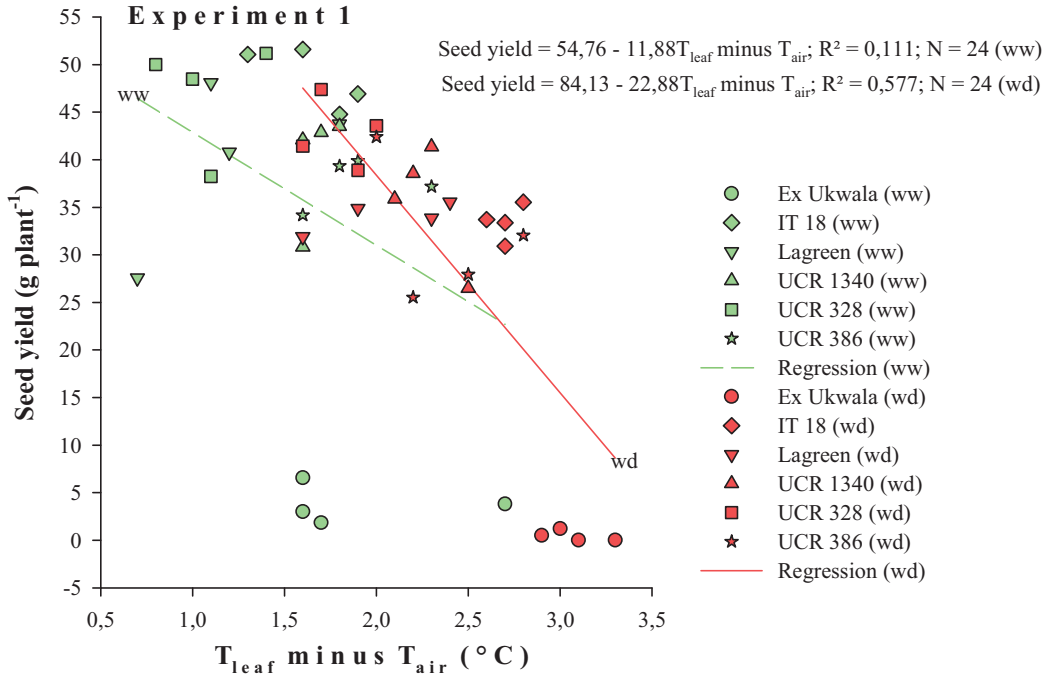

Fig A3: Regression analysis of T_{leaf} minus T_{air} (ΔT) against seed yield under well-watered (ww) and water deficit (wd) conditions in experiment 1

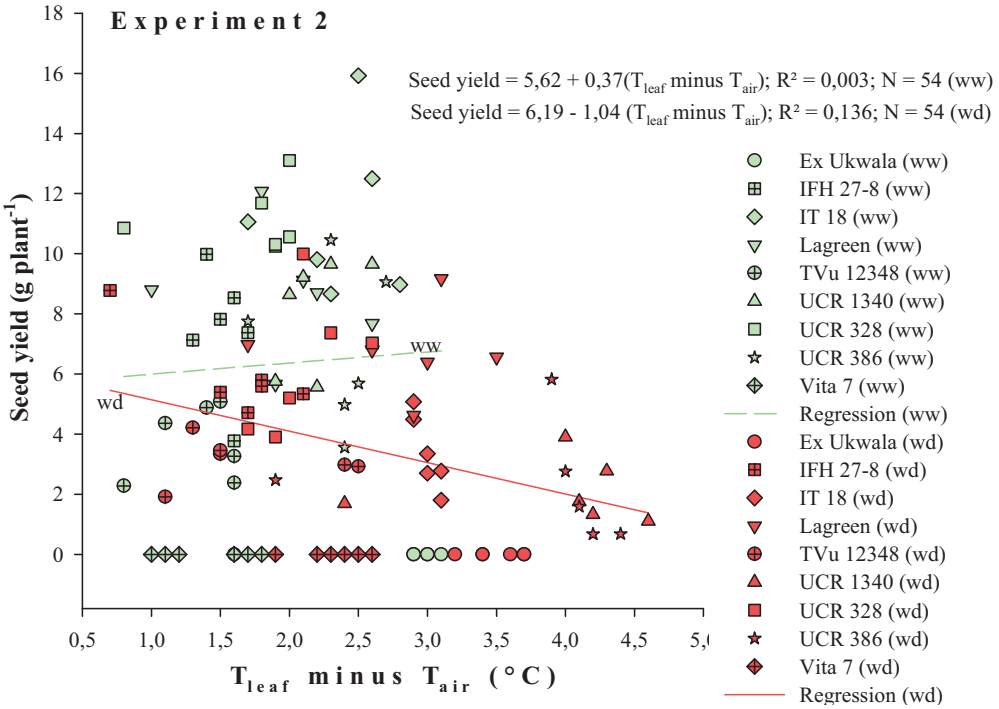

Fig A4: Regression analysis of T_{leaf} minus T_{air} (ΔT) against seed yield under well-watered (ww) and water deficit (wd) conditions in experiment 2

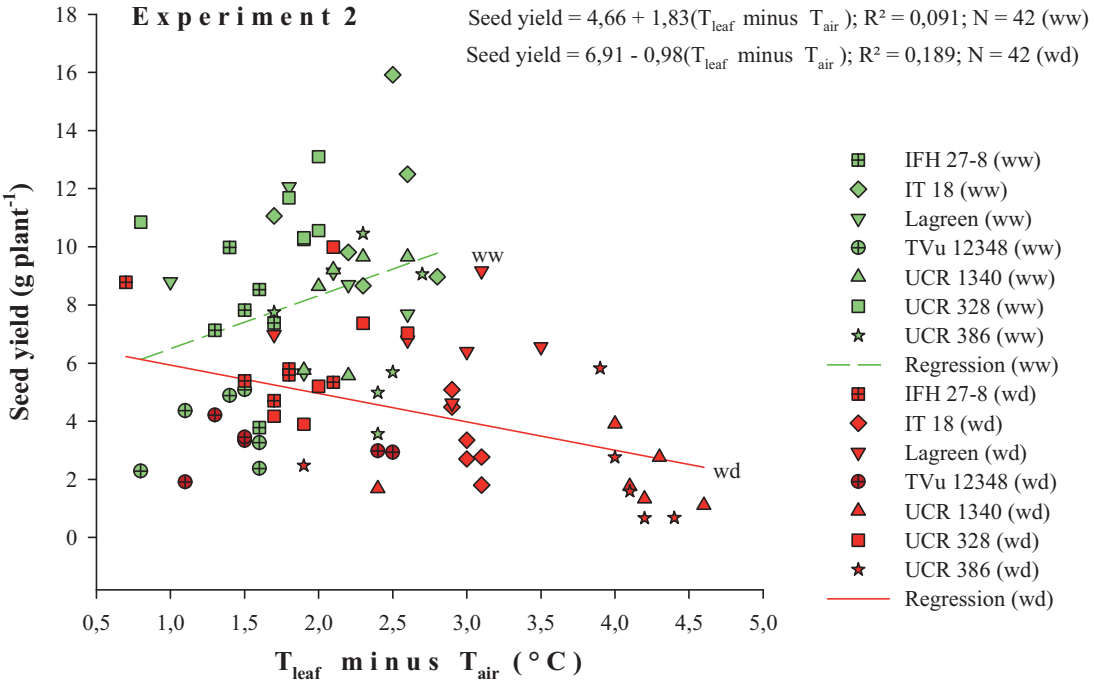

Fig A5: Regression analysis of T_{leaf} minus T_{air} (ΔT) against seed yield under well-watered (ww) and water deficit (wd) conditions in experiment 2 (without Ex Ukwala and Vita 7)