

Full Length Research Paper

# Water relations, gas exchange characteristics and water use efficiency in maize and sorghum after exposure to and recovery from pre and post-flowering dehydration

Abuhay Takele<sup>1\*</sup> and Jill Farrant<sup>2</sup>

<sup>1</sup>Melkassa Agricultural Research Center, P. O. Box 436, Nazret, Ethiopia.

<sup>2</sup>University of Cape Town, Department of Molecular and Cell Biology, Private bag 7701, Rondebosch, Cape Town, South Africa.

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The effect of dehydration and rehydration at pre and post-flowering stages on the water relations, gas exchange characteristics (stomata conductance, photosynthesis and Fv/Fm (quantum efficiency) ratio), pigment compositions (chlorophyll and carotenoid contents) and water use efficiency on maize (cv Melkassa-2) and sorghum (cv Macia) were investigated with the objectives of understanding the physiological basis of drought resistance mechanisms and investigating whether there were differential responses in some of the physiological traits of drought resistance and recovery upon rehydration of maize and sorghum. The study was carried out in a controlled environment growth chamber under constant environmental conditions (12/12 h day/night, 28-32/17°C day/night temperature, 60-80% RH and PPFD of 1200-1400  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ). Both species showed reduced  $g_s$  (stomatal conductance) in response to dehydration to reduce water loss over a range of relative water contents during both developmental stages. In maize, stomata appeared to be closed earlier and completely, while partial stomatal closure at relatively higher relative water contents appeared to have occurred in sorghum.  $g_s$  recovery occurred following pre-flowering rehydration to the control level in both species only. The response of all other gas exchange characteristics ( $P_n$  and Fv/Fm) and water use efficiency followed similar trends to that of  $g_s$  both in maize and sorghum at pre and post-flowering dehydration and rehydration. Dehydration also led to a decrease in Fv/Fm ratios as compared to the control plants in both species. Both species, however, exhibited similar rates of Fv/Fm ratios during pre and post-flowering dehydration. Fv/Fm ratios appeared to be affected more during post than pre-flowering dehydration in both species. Fv/Fm ratios of both species were recovered following pre-flowering rehydration but only maize recovered from post-flowering rehydration.

**Key words:** Chlorophyll, carotenoid, dehydration, electrolyte leakage, rehydration, stomatal conductance.

## INTRODUCTION

Water deficit is the most common adverse environmental factor limiting crop production in the dry land areas of Africa. In these areas, maize and sorghum are very

important staple crops. They are grown across a range of agro-ecological zones where shortages of water resulting from low and erratic rainfall is a major constraint for crop

production (Rosenow et al., 1997).

Crop plants when exposed to water deficits undergo physiological, morphological and biochemical changes in order to survive. The changes that occur at various levels of plant organization (cellular, molecular, etc.) in response to drought stress are considered to be adaptation mechanisms (Turner, 1997). Several workers have examined the response of different crops to water deficits and have identified various traits that confer drought resistance in cereals (Blum, 1989; Ludlow and Muchow, 1990; Turner, 1997). These include maintenance of high water potential, control of stomatal behaviour and osmotic adjustment under drought conditions (Blum, 1988; Ludlow and Muchow, 1990). Genotypes differ in their ability to recover upon rehydration and the ability of a genotype to recover from stress is closely related to its hydration status prior to recovery (Malabuyot et al., 1985).

Genetic variation in leaf water potential, stomatal conductance and photosynthetic rate have been reported in several crop species (Peng and Kreig, 1992). These traits might be used to select superior cultivars or crop species with the ability to maintain high plant water status, high stomatal conductance and maintenance of photosynthetic rate under water deficit conditions. The selection of such physiological traits in the improvement programs of crop plants, however, requires the establishment of significant association between various traits and drought resistance. More detailed understanding of the physiological adaptations enabling superior performance of crop species and/or genotypes under drought stress and/or required for the maintenance of physiological activities for growth and productivity during periods of recovery from stress upon rehydration will ultimately help in the selection and promotion of drought tolerant crop species. This is particularly relevant for crops such as sorghum and maize, which are predominantly grown in marginal rainfall regions of the world.

This study was, therefore, carried out with the objectives of understanding the physiological basis of drought resistance mechanisms in maize and sorghum and investigating whether there were differential responses in some of the physiological traits of drought resistance and recovery upon rehydration of maize and sorghum. Measurements were taken on plant water relations, gas exchange characteristics, Fv/Fm and water use efficiency of maize and sorghum after exposure to and recovery from pre and post-flowering dehydration.

## MATERIALS AND METHODS

### Growth conditions and treatment

Maize seeds (*Zea mays* L.) (cv *Melkassa-2*) and sorghum (*Sorghum bicolor* Moench L.) (cv *Macia*) were obtained from the

Maize Improvement Program for Moisture Stress Areas, Melkassa Agricultural Research Centre, Ethiopia and ICRISAT Centre, Bulawayo, Zimbabwe, respectively. The experiment was conducted in a controlled chamber under constant environmental conditions (12/12 h day/night, 28-32/17°C day/night temperature, 60-80% RH and PPFD of 1200-1400  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) at the Department of Botany, University of Cape Town. The following was done for both species. To ensure emergence, 5 seeds were sown in plastic pots, each was 31 cm deep with an internal diameter of 18 cm. About 10 kg of sandy loam soil was used for each pot. Emergence occurred 5-7 days after planting (DAP). 20 Days after emergence, the pots were thinned to 2 seedlings of uniform size per pot. Plants were watered frequently to avoid the development of any moisture deficit. At 60 (pre-flowering) and 90 (post-flowering, grain filling stage) days after emergence, 2 watering treatments were applied: either maintained fully hydrated (control) or dehydrated treatments. Control plants were regularly watered to field capacity (F.C) to avoid any development of water stress and the dehydration was induced by withholding water for 20 days at each growth stages. At the end of each dehydration treatment, plants were rehydrated by soil watering (as for the control plants) for another 20 days and their recovery was studied. 3 pots of each species in each treatment represented 3 replications. 5 different samples were taken during the dehydration period at each different growth stage and during recovery, respectively. Each pot was given P and N at the rate of 0.80 g/pot (150 kg/ha) and 1.1 g/pot (200 kg/ha), respectively. Single super phosphate and lime ammonium nitrate were used as source of P and N, respectively.

At regular interval during the entire cycle (pre and post-flowering dehydration), water relations, gas exchange characteristics and water use efficiency were measured. The same measurements were performed on control plants which remained hydrated throughout.

### Plant water relations

Water status of both species was determined by measuring the relative water content. Relative water content was calculated using the method of Henson et al. (1981) as:

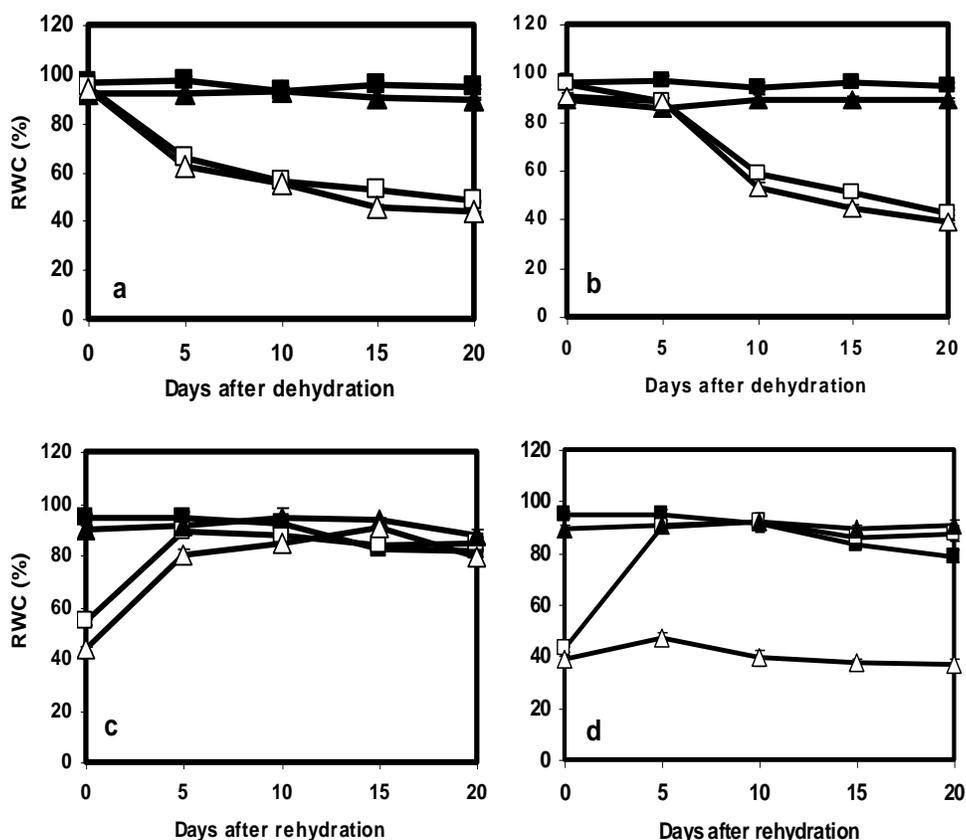
$$\text{RWC (\%)} = [(\text{FW}-\text{DW}) / (\text{TW}-\text{DW})] \times 100$$

Where, FW represent fresh weight, DW is the dry weight and TW the turgid weight. Turgid weight was determined after floating leaf segments in distilled water in sealed vials for 24 h at room temperature, and oven dried at 70°C for 48 h.

### Gas exchange parameters

At each growth stages during dehydration and rehydration, the gas exchange physiology [stomatal conductance ( $g_s$ ), photosynthesis ( $P_n$ ) and transpiration (E)] of fully expanded intact leaves of upper canopy were recorded using a portable infrared gas analysis (IRGA) system (LCA-3, the Analytical Development Corporation, Hoddeston, England). Photosynthetic water use efficiency (WUE) was estimated as the ratio of photosynthesis rate to transpiration rate.

Chlorophyll fluorescence was measured using the leaves for the measurement of gas exchange, by a modulated portable fluorometer (os-500:opti-sciences, USA) and by calculating the quantum efficiency of leaves at various stages of dehydration and recovery during rehydration. The initial  $F_0$ , and maximum fluorescence,  $F_M$ , using a saturating light intensity of approximately 4  $\mu\text{mol photons m}^{-2}\text{s}^{-1}$  and duration of 1 s, was measured.  $F_v$  was



**Figure 1.** Changes in mean relative water content (%) of maize (a, c) and sorghum (b, d) during pre (■, □) and post-flowering (▲, △) dehydration (a, b) and rehydration (c, d), respectively. ■ and ▲ represent control and □ and △ represent dehydration/rehydration treatments. Vertical bars denote standard errors of means (n=3).

obtained by subtracting  $F_0$  from  $F_M$  and  $F_v/F_M$  was calculated.

### Statistical analysis

Statistical analyses were carried out using STATISTICA for windows version 6.0, Statsoft, Inc, USA. The results presented were the mean of 3 replicates. In all figures, the scores of the mean were calculated and significances between treatments as well as between the 2 species were tested by factorial analysis of variance and Duncan's multiple range tests at the 5% level of significance. Standard errors were represented as vertical bars.

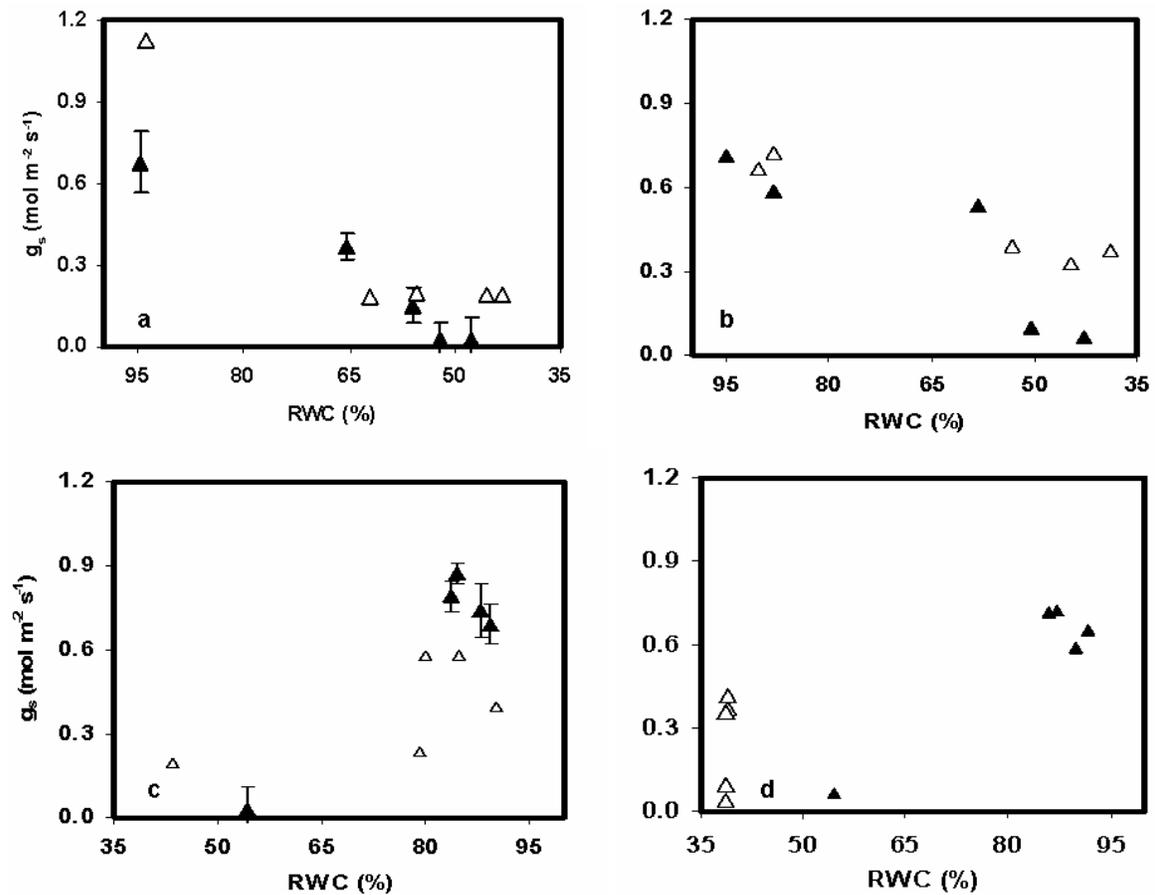
## RESULTS

### Leaf relative water content (RWC %)

Dehydration caused a significant ( $P < 0.05$ ) decrease in the relative water content of both species during both pre and post-flowering stages (Figure 1a and b). The difference between the 2 species was significant for the

first 5 days after withholding water. Relative water content of dehydrated maize plants decreased rapidly for the first 10 days and then slowly but steadily. In contrast to maize, there was almost no change in the RWC of sorghum plants for the first 5 days under the prevailing dehydration conditions but thereafter, there was a sharp decrease to the level equivalent to the values of maize plants. Mean relative water content during dehydration was reduced from the initial full turgor value of 94 and 93% to 46 and 41% in maize and sorghum at the end of dehydration, respectively.

Visual observations indicated that in maize, leaf rolling was displayed within 5 days (corresponding to relative water content of 82%) of pre-flowering dehydration and then as the dehydration process progressed, leaf rolling was more tightened. In contrast, visible leaf turgidity was maintained in sorghum for at least 12 days after initiation of dehydration and then leaf rolling was initiated at approximately relative water content of 76%. During post-flowering dehydration, leaf rolling as a dehydration avoidance mechanism was not displayed in either species.



**Figure 2.** Changes in mean stomatal conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ ) of maize (a and c) and sorghum (b and d) during pre (▲) and post-flowering (Δ) dehydration (a, b) and rehydration (c, d) as related to RWCs, respectively. Vertical bars denote standard errors of means ( $n=3$ ).

Relative water content of both crops returned to control values within 5 days of rehydration during pre-flowering rehydration, but only maize rose to full recovery during post-flowering rehydration (Figure 1c and d).

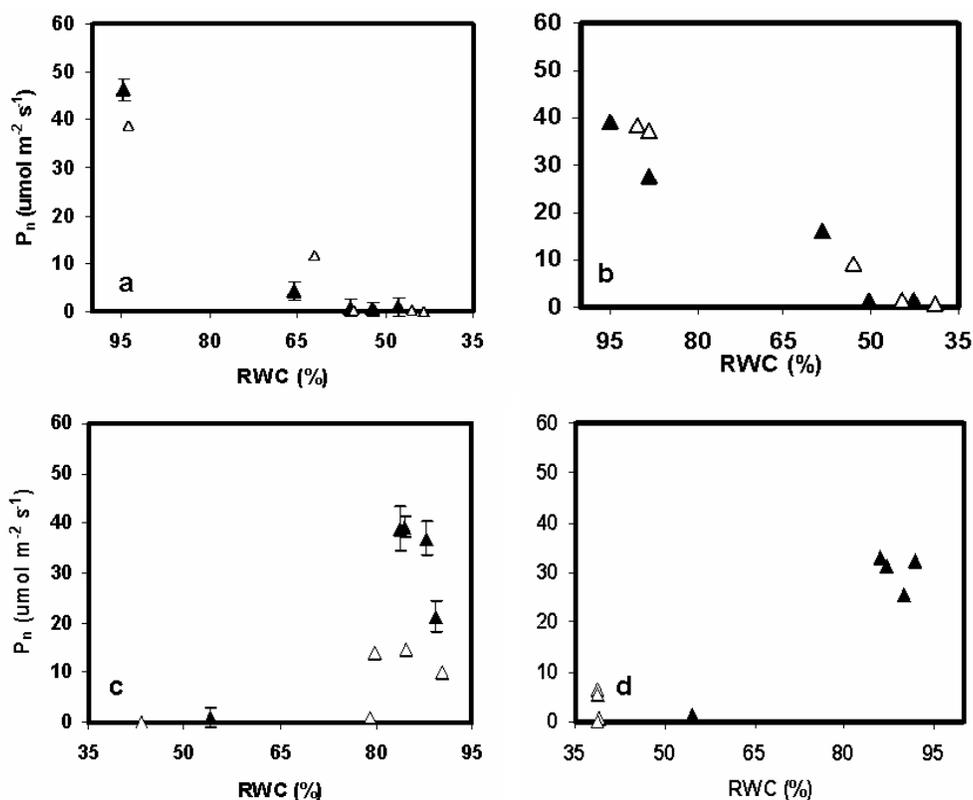
## Gas exchange characteristics

### Stomatal conductance

Dehydration during both pre and post-flowering stages significantly decreased stomatal conductance of both species (Figures 2a and b). Differences in stomatal conductance of both species were observed between pre and post-flowering dehydrated plants. In maize, differences occurred at the beginning of the measurement period approximately at RWC of 95% and between RWC of 53 and 48% when conductance of post-flowering dehydrated plants was significantly ( $p<0.05$ ) higher than pre-flowering dehydrated plants. Differences

in stomatal conductance of sorghum between pre and post-flowering dehydrated plants became evident towards the end of the treatment period between RWC of 58 and 39% at which point the post-flowering dehydrated plants showed significantly ( $p<0.05$ ) higher stomatal conductance values than pre-flowering dehydrated plants (Figure 2b).

Corresponding to the decrease in RWC, the patterns of changes of stomatal conductance differed between species during pre and post-flowering dehydration. Stomatal conductance of maize that underwent post-flowering dehydration, showed a dramatic decrease between RWC of 95 and 64% within 5 days of withholding water after which it remained without any significant change between RWC of 64% and 48% at the final stage of dehydration. In contrast to maize, after an initial decrease, approximately between RWC of 95 and 88%, stomatal conductance of sorghum plants during pre-flowering dehydration showed no remarkable change between RWC of 88 and 58% and then conductance



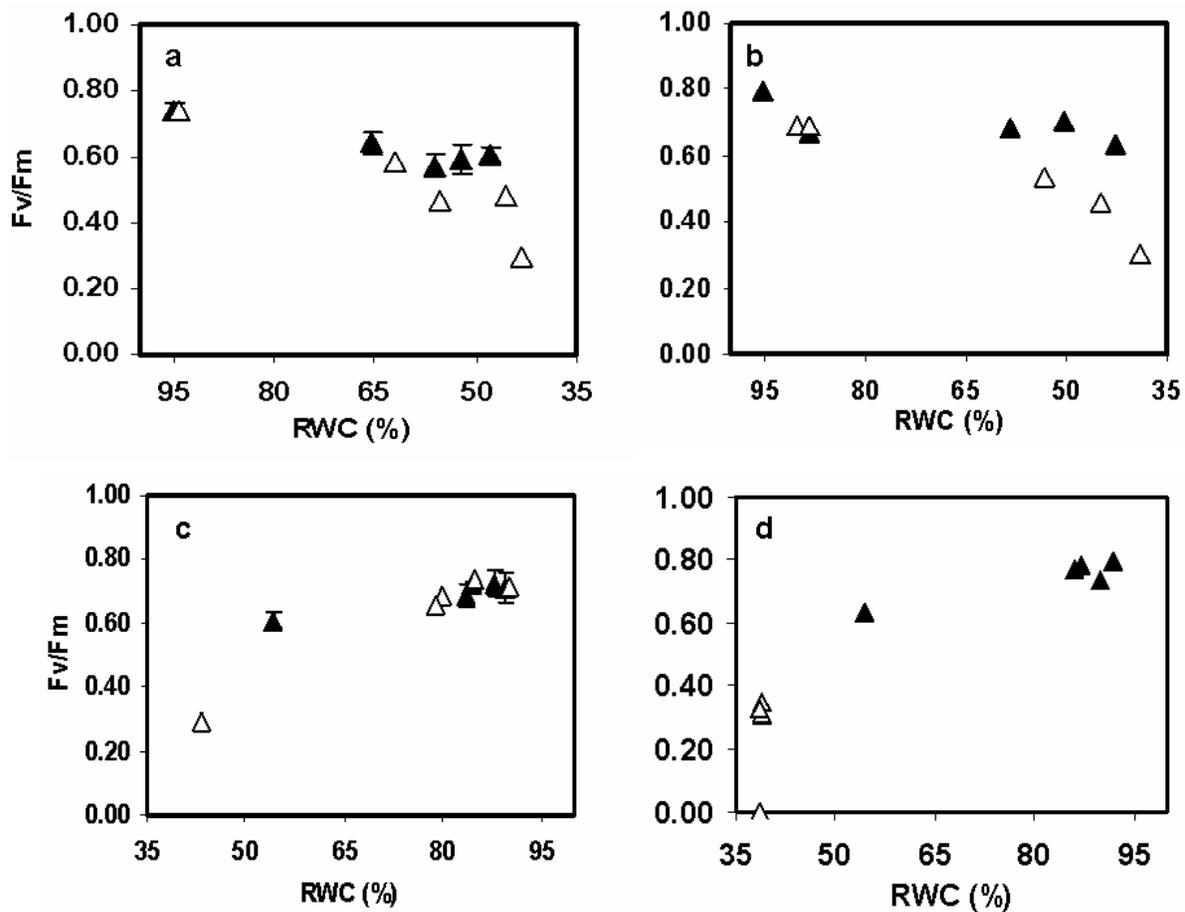
**Figure 3.** Changes in mean photosynthesis rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) of maize (a, c) and sorghum (b, d) during pre (▲) and post-flowering (△) dehydration (a, b) and rehydration (c, d) as related to RWCs, respectively. Vertical bars denote standard errors of means (n=3).

decreased most markedly until the end of the experiment. Between RWC of approximately 88 and 53%, the decrease in stomatal conductance of post-flowering dehydrated sorghum was rather gradual and thereafter conductance showed little change until RWC reached 39% at the final phase of dehydration.

After 5 days of rehydration, stomatal conductance of maize fully recovered at about 88% RWC following pre-flowering rehydration (Figure 2c). Recovery in the stomatal conductance of pre-flowering rehydrated sorghum was rather slow and full recovery occurred at approximately 90% of RWC (%) at the final phase (20 days after rehydration began) of rehydration (Figure 2d). Approximately 55% of stomatal conductance in maize that underwent post-flowering rehydration resumed at 80% of RWC 5 days after rehydration began but stomatal conductance showed a steady decrease 10 days after post-flowering rehydration. There was no change in stomatal conductance of sorghum from that measured at the end of post-flowering dehydration for the first 10 days after rehydration commenced but thereafter, conductance decreased to almost zero at the end of the rehydration period.

### Photosynthesis rate ( $P_n$ )

Dehydration during pre and post-flowering stages caused a considerable decrease in photosynthesis rate of both species (Figures 3a and b). Differences in the patterns of changes in photosynthesis rate were noted between pre and post-flowering dehydrated plants with changes in RWC in both species. In maize, differences between pre and post-flowering dehydrated plants were evident approximately between RWC of 95 and 65% when photosynthesis rate of pre-flowering dehydrated plants decreased more markedly than post-flowering dehydrated plants (Figure 3a). In sorghum, photosynthesis rate of pre-flowering dehydrated plants decreased continually until the end of the dehydration period whereas photosynthesis rate of plants that underwent post-flowering dehydration was maintained without changes for the first 5 days of dehydration approximately between RWC of 93 and 88%. With further decrease in RWC, photosynthesis rate was negligible after 10 days of dehydration (Figure 3b). Significant ( $p < 0.05$ ) difference between species in the sequence of changes in photosynthesis rate was also observed in



**Figure 4.** Changes in mean quantum efficiency of maize (a, c) and sorghum (b, d) during pre (▲) and post-flowering (△) dehydration (a, b) and rehydration (c, d) as related to RWCs, respectively. Vertical bars denote standard errors of means ( $n=3$ ).

response to pre and post-flowering dehydration.

In maize, as RWC dropped from 95 to 55% within 5 days after the initiation of dehydration, the decrease in photosynthesis rate ranged from  $46.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  to  $0.7 \mu\text{mol m}^{-2} \text{s}^{-1}$  during pre-flowering dehydration and from  $39.0 \mu\text{mol m}^{-2} \text{s}^{-1}$  to  $0.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  during post-flowering dehydration. In contrast, at similar RWC, the decrease in the photosynthesis rate of sorghum was from  $39.2 \mu\text{mol m}^{-2} \text{s}^{-1}$  to  $16.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  and from  $38.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  to  $9.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  during pre and post-flowering dehydration, respectively.

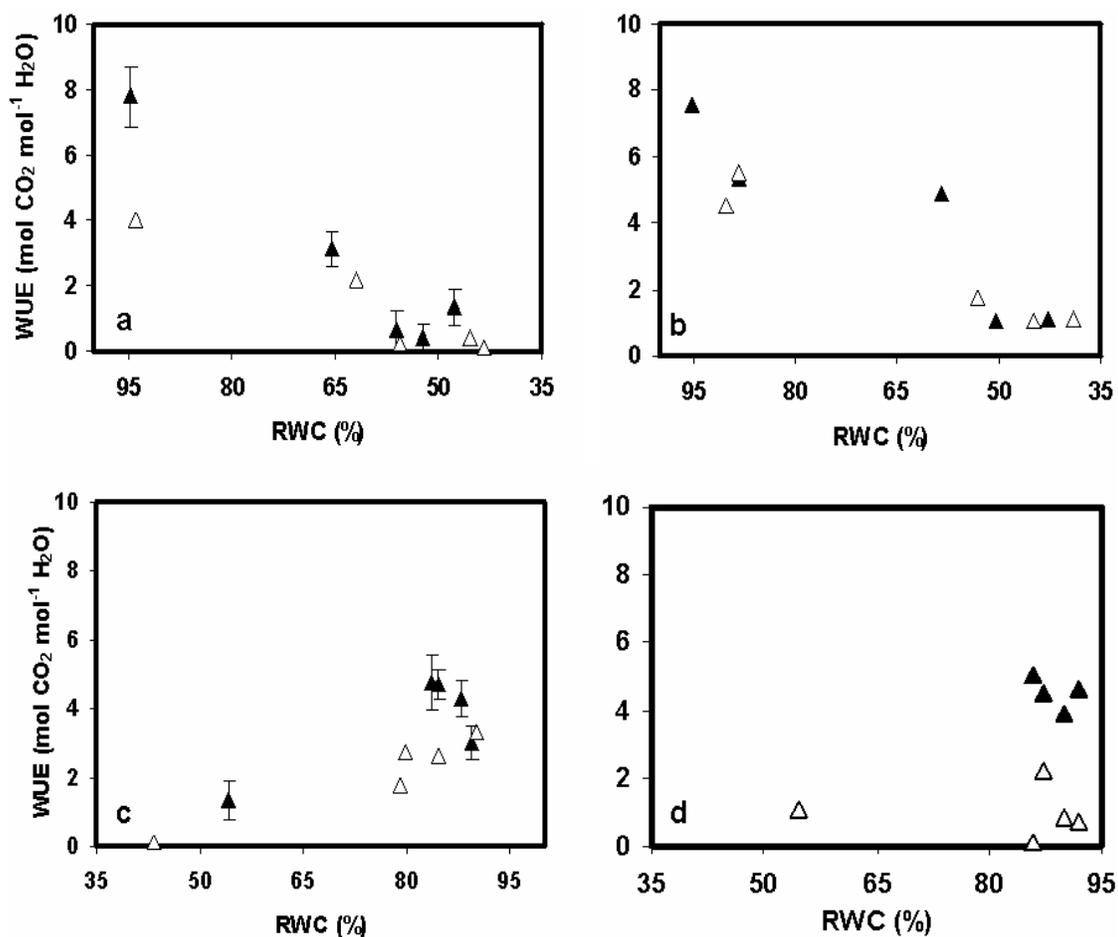
There was a noticeable difference in the patterns of response in photosynthesis rate between pre and post-flowering rehydrated plant in both species (Figures 3c and d). Photosynthesis rate of pre-flowering dehydrated maize fully resumed 10 days after rehydration began and that of post-flowering dehydrated plants showed an initial increasing trend following rehydration, but with further increase in RWC (%), photosynthesis rate rather decreased until the end of the rehydration period.

Sorghum on the other hand exhibited only 75% recovery until the end of rehydration period but post-flowering rehydrated plants did not show any noticeable change until the end of the rehydration period (Figures 3c and d).

#### Quantum efficiency of photosystem II (Fv/Fm)

Dehydration during pre and post-flowering stages caused a significant ( $p<0.05$ ) decrease in Fv/Fm ratio of both species as compared to the well watered plants, indicating that dehydration caused a direct effect on the PSII photochemistry (Figures 4a and b). There were slight differences in the patterns of the changes in Fv/Fm ratio between pre and post-flowering dehydration in both maize and sorghum.

During pre-flowering dehydration, there was a gradual but consistent decrease in the Fv/Fm ratio of both species. In contrast, during post-flowering dehydration, when RWC decreased below 65%, there was a large and



**Figure 5.** Changes in mean water use efficiency ( $\text{CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ ) of maize (a, c) and sorghum (b, d) during pre ( $\blacktriangle$ ) and post-flowering ( $\triangle$ ) dehydration (a, b) and rehydration (c, d) as related to RWCs, respectively. Vertical bars denote standard errors of means (n=3).

much faster decrease. The magnitude of the effect of pre and post-flowering dehydration on Fv/Fm ratio was similar for the 2 species. When Fv/Fm ratio was expressed in relation to the initial value, there were 18 and 20% reduction during pre-flowering dehydrated maize and sorghum at the end of the dehydration cycle, respectively. In contrast, during post-flowering dehydration, the reduction in Fv/Fm ratios was 60 and 56% in maize and sorghum at the end of the dehydration period, respectively.

Maize recovered to the control level as soon as rehydration began during both pre and post-flowering rehydration (Figure 4c). Similar to maize, Fv/Fm of sorghum was restored to the pre water stress level within 5 days of pre-flowering rehydration, but there was no change in the Fv/Fm ratio from that measured during post-flowering dehydration until day 15 and thereafter, Fv/Fm rather decreased with further rehydration (Figure 4d).

### Water use efficiency

Dehydration significantly ( $P=0.05$ ) decreased photosynthetic water use efficiency (the ratio of  $P_n$  to transpiration rate) in both species (Figure 5a and b). The decrease in water use efficiency was mainly due to greater dehydration induced reduction in  $P_n$  than transpiration. There was a significant difference between the tested species for water use efficiency in response to dehydration. Dehydration induced decrease in water use efficiency in maize by 63% and that of sorghum by only 37%. Time course of the changes over the period of dehydration in both species followed similar patterns to those of  $P_n$  and transpiration rate. When a pattern of response over the duration of dehydration was considered, there was a dramatic decrease in water use efficiency in maize until day 15 of the onset of dehydration. In contrast, water use efficiency in dehydrated sorghum plants was up to the level of the

control plants in the first phase but there was a rapid decrease 5 days after imposition of dehydration. Mean of water use efficiency was not significantly different between pre and post-flowering dehydration. The magnitude of the changes in water use efficiency over the duration of dehydration period was similar for both pre and post-flowering stages.

Recovery of water use efficiency upon rehydration was slow for both species and in maize it attained fully hydrated level after 15 days of rehydration after which there was a decrease while in sorghum, approximately 50% of water use efficiency was recovered after 20 days of rehydration (Figures 5c and d).

## DISCUSSION

### Differences in physiological responses to dehydration between maize and sorghum

The 2 crops differed in the rate of change in RWC immediately after withholding water (Figure 1). As evapotranspiration from the limited volume of soils in the pots of maize became high, there was a sharp decrease in the soil water contents and the leaves experienced a shortage of water supply. RWC decreased quickly both during pre and post-flowering dehydration (Figure 1). The fast rate of development of plant water deficits in maize than sorghum induced early leaf rolling (data not shown) and stomatal closure (Figure 2) in the former than the latter.

Variation in stomatal conductance is a more sensitive indicator for selecting desirable cultivars and crop species. This study indicated that both maize and sorghum showed reduced stomatal conductance to reduce water loss continuously over a range of RWC and duration of pre and post-flowering dehydration. However, there was a difference in the extent of response of stomatal conductance between maize and sorghum with changes in RWC. During both pre and post-flowering dehydration, drought resistance in maize was achieved through complete stomatal regulation, while partial stomatal closure at relatively higher values of RWC appeared to have occurred in sorghum (Figures 2a, b and inset). Dehydration-induced stomatal regulation in maize was also earlier reported (Premachandra et al., 1992; Stikic and Davies, 2000). However, despite complete stomatal regulation and early onset of leaf rolling, maize exhibited fast rate of decrease in RWC. Under dehydration conditions, stomatal closure could be triggered by both changes in chemical signalling and/or hydraulic status of the plant (Tardieu and Davies, 1992). Chemical messages, mainly ABA originating from roots and transferred to the leaf through the transpiration stream may cause stomatal closure regardless of the  $\psi_L$  (leaf water potential) of the plant (Davies and Zhang, 1991).

Decrease in stomatal conductance could improve the stability of yield, because it reduces water loss and lowers the probability of exhausting soil water before maturity. Alternatively, since stomata controls gas exchange, dehydration avoidance achieved through stomatal closure in plants reduces productivity (Ludlow and Muchow, 1990). The parallel decrease in gas exchange characteristics (photosynthesis rate and Fv/Fm ratios) in both species at approximately between RWC of 93 and 65% during both pre and post-flowering dehydration strongly support stomatal closure as the major factor in reducing photosynthesis (Chaves, 1991; Cornic, 1994). The greater decrease in photosynthetic rate (Figures 3a and b) of maize was probably attributed to the much faster decrease in RWC which induced early leaf rolling and effective stomatal closure. Sorghum on the other hand was able to use water more efficiently by maintaining relatively higher RWC, delayed leaf rolling for extended period and stomata remained partially open altogether allowing a relatively higher photosynthesis rate. Stomatal closure is considered to be responsible for the decrease in photosynthetic rate in several crop species exposed to moderate water deficits (Cornic, 1994) and there was no indication of damage to chloroplast reactions (Sharkey and Seemann, 1989).

Under more severe dehydration however, reduced photosynthesis rate is generally considered to be due to non-stomatal factors (Lawlor, 1995; Lawlor and Cornic, 2002). The decrease in photosynthesis rate of both maize and sorghum to almost zero below RWC of approximately 65% during the late phase of dehydration period, and subsequent lack of recovery upon rehydration may suggest that factors other than stomatal limitation might have been involved. Several studies suggest that the ratio of Fv/Fm gives a direct estimate of the yield of PSII photochemistry (Kicheva et al., 1994; Liang et al., 1997). A sustained decrease in Fv/Fm is believed to indicate the occurrence of photo inhibitory damage, in response to many environmental stresses including water deficit stress (Maxwell and Johnson, 2000). In this study, the observed decrease in the ratio of Fv/Fm in pre and post-flowering dehydrated maize and sorghum (Figures 4a, b and inset) supported the idea that dehydration during both developmental stages in maize and sorghum had a direct effect on the PSII photochemistry. The results of this study are in agreement with the findings of Massacci et al. (1996) who reported that the inhibition of photosynthesis rate by dehydration was due to non-stomatal factor in field grown sweet sorghum.

Stomatal regulation controls the exchange of water and carbon between the leaf and the atmosphere and thus affects water use efficiency (Blum, 1988). In this study, the faster rate of decrease observed in the water use efficiency (Figure 5a) of maize may have been attributed to the early and complete stomatal closure which in turn resulted to a greater decrease in  $P_n$  than transpiration.

Sorghum by retaining green leaf area for an extended period during pre and post-flowering dehydration was better able to maintain relatively higher water use efficiency than maize. In this case, higher water use efficiency was due to increased photosynthetic rate during both pre and post-flowering dehydration (Figure 3). Therefore in the present study water use efficiency, which indicates the tissue water relation of a species, suggests differences in adaptation strategies to dehydration between the 2 species.

### **Differences between pre and post-flowering growth stages in response to dehydration in maize and sorghum**

The expression of drought tolerance in crop plants is dependent on the stage of development at which the stress occurs (Blum, 1988; Tuinstra et al., 1997). For example, in sorghum developmentally specific patterns of drought tolerance have been identified and symptoms of susceptibility during each stage have been characterized (Rosenow et al., 1997). It has been proposed that growth stage had a major effect on stomatal sensitivity to dehydration and this has been demonstrated in maize and sorghum (Ackerson and Krieg, 1977; Garrity et al., 1984) at which stomatal response was totally insensitive during the reproductive stage. This change in stomatal sensitivity with crop age was suggested to be due to osmotic adjustment which would allow the plant to maintain cell turgor and open stomata under low leaf water potentials (Ackerson and Krieg, 1977). However, the results of the present study indicated that stomatal response of both maize and sorghum at both pre and post-flowering dehydration were sensitive to the decrease in the relative water contents over the duration of dehydration cycle (Figure 2). This is in agreement with Massacci et al. (1996) who reported that stomata did not show decreasing sensitivity to drought stress during plant development in field grown sweet sorghum.

So far, the influence of dehydration on Fv/Fm ratio has usually been examined in the early developmental stages of plants and experimental data are scarce for comparison with the results from dehydration at pre and post-flowering stages, although the available reports indicate that the way Fv/Fm changes with dehydration strongly depend with plant age (David et al., 1998; Massacci et al., 1996). In the present study, dehydration during pre and post-flowering stage exerted differing effects on the Fv/Fm ratio of both species with the effect being much more pronounced below RWC of 65% during the late phase of post-flowering dehydration (Figures 4a and b). Hence the contribution of non-stomatal factors to explain drought induced depression in photosynthesis may be expected to increase with plant age, and our results are in accordance with this hypothesis.

The result reported in this study is consistent with the findings of Massacci et al. (1996).

### **Differences in the physiological responses to rehydration between maize and sorghum**

Despite the fact that rehydration following pre and post-flowering dehydration is a determinant to stabilize grain yield in cultivated crop plants, there is a lack of literature concerning the effect of rehydration on the physiological response of crop plants at pre and post-flowering stages. The understanding of the recovery of gas exchange characteristics (stomatal conductance and photosynthesis rate) and the processes which controls it, is therefore poorly understood at different developmental stages in general and at pre and post-flowering stages in particular at which water deficits exerts the greatest loss of grain yield. The rehydration experiment indicates that the ability of stomatal conductance to recover after stress relief decreases with plant age. As shown in Figures 2c and d, although maize attained full recovery, the rate of recovery of stomatal conductance during pre-flowering rehydration was slow and sorghum did not attain full recovery. These findings are in accordance with the findings of Ludlow et al. (1980) who reported that recovery of stomatal conductance upon rewatering was slow and incomplete. During post-flowering stage, although there was an initial recovery, rehydration accentuated the negative effect of dehydration on stomatal conductance of both maize and sorghum (Figure 2). These results indicate that under the condition of dehydration that prevailed in this work, rehydration of the species under investigation at the later reproductive stage was apparently deleterious than pre-flowering stage. It appeared that except during post-flowering rehydration in sorghum where RWC did not improve upon rehydration, the rate of recovery of stomatal conductance was not determined by the rate at which RWC recovered during pre and post-flowering rehydration in maize and pre-flowering rehydration in sorghum, since full recovery of RWC was attained during the periods. According to Ludlow et al. (1980) the slow rate of recovery of stomatal conductance to the level of control plants results from accumulation of abscisic acid. This could be the reason why there was a slow rate of recovery in both species during pre-flowering rehydration. The absence of recovery during post-flowering rehydration in both maize and sorghum may be associated with the harmful effect of rehydration at the maturity stage of both species. The lack of recovery of stomatal conductance also exerted an influence on the recovery of photosynthesis rate (Figure 3) and water use efficiency (Figure 5).

During pre and post-flowering stage in maize and during pre-flowering stage in sorghum, when plants were fully rehydrated, the Fv/Fm ratio returned to the control

level and the photosynthetic apparatus and cell membranes were repaired completely (Figures 4c and d). However, after an apparent initiate repair, the rapid decrease in Fv/Fm ratio (Figure 4d) during post-flowering rehydration in sorghum suggest that rapid rehydration may be as harmful to the photosynthetic apparatus as the dehydration itself during post-flowering stage.

## Conclusion

The results of this study pointed out the need for using integrated traits when evaluating drought resistance of plants. The results showed that the maize cv Melkassa-2 and sorghum cv MACIA had a remarkable array of contrasting behaviour in response to pre and post-flowering dehydration and rehydration. Differences in maintenance of RWC may be related to performance under dehydration, particularly when crop species of different adaptation were compared under stress conditions of varied intensity. This was observed particularly during moderate water deficits when sorghum exhibited relatively higher RWC during both pre and post-flowering dehydration. In conclusion, sorghum appeared to be more resistant to moderate pre and post-flowering dehydration than maize; this can be attributed to its greater capability to maintain relatively higher RWC and consequently delay leaf rolling, maintain stomata partially open, maintain  $P_n$  at a reduced rate and relatively higher water use efficiency. Both species, however, were found to be susceptible to severe pre and post-flowering dehydration.

This study will help in the understanding of some adaptive mechanisms developed by maize and sorghum and contribute to the identification of useful traits for breeding programs.

However, further studies are necessary under field conditions to clarify the adaptive responses in both maize and sorghum during pre and post-flowering dehydration and the capacity to return to normal physiology during post-stress rehydration.

**Abbreviations:** Fv/Fm, Quantum efficiency ratio;  $g_s$ , stomatal conductance;  $P_n$ , photosynthesis.

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