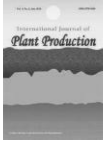

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Effect of a short and severe intermittent drought on transpiration, seed yield, yield components, and harvest index in four landraces of bambara groundnut

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Abstract

Drought is a major constraint to crop production worldwide and landraces are one of the important genetic resources to crop improvement in the dry areas. The objective of this study was to investigate transpiration and yield responses of bambara groundnut (*Vigna subterranea* L. Verdc.) landraces exposed to a intermittent drought spell at an early reproductive stage. The four landraces (S19-3, Uniswa Red, LunT, and Ramayana collected from Namibia, Swaziland, Sierre Leone, and Indonesia, respectively) were grown in pots in a climate-controlled greenhouse and were either well-watered (WW) daily to 90% of pot holding capacity until seed maturity or drought-stressed (DS) in the period from 76 to 85 days after sowing (flowering and early podding stage). During drought, although the total water use differed among the four landraces, transpiration rate and stomatal conductance (g_s) responded similarly to soil drying. The high soil water thresholds for the reduction of transpiration rate and g_s of bambara groundnuts indicate their great sensitivity in the stomatal control over plant water loss during soil drying. Even though the shoot dry weight at maturity was hardly affected by DS, seed yield, seed number, and harvest index were all significantly decreased in the DS plants. Among landraces, LunT and Ramayana were more susceptible to DS than S19-3 and Uniswa Red in terms of reduction of seed number and seed yield. The different responses of the landraces to DS may reflect their adaptation to their local climate at the site of collection being that landraces collected from wet regions were more vulnerable to DS than those collected from dry areas.

Keywords: Harvest index; Drought stress; Landraces; Stomatal conductance; Seed yield.

Introduction

Bambara groundnut (*Vigna subterranea* L. Verdc.) is an indigenous grain legume grown mainly by subsistence farmers in Sub-Saharan Africa. The crop is also grown in parts of South and Central America, South and South-East Asia and Northern Australia (Linnemann and Azam-Ali, 1993). The seed of the crop is very nutritive, as it contains sufficient quantities of proteins, carbohydrates and lipid (Brough and Azam-Ali, 1992; Yusef et al., 2008). Bambara groundnut has long been considered a drought resistant crop (Ntundu et al., 2006), and the crop can produce some relative greater seed yield as compared with other legumes under similar drought conditions (Babiker, 1989). Thus, extension of bambara groundnut cultivation for drought-prone regions is encouraging in sustaining food and nutrients supply for poor farmers. However, to fully explore the potential of bambara groundnuts cultivation, more knowledge about the mechanisms underlying their adaptation to drought is required (Collinson et al., 1997); particularly, investigations on the landrace diversity in drought tolerance are necessary for selecting and breeding high yielding landraces/cultivars to drought-prone regions.

Drought may affect crop growth and physiology at any developmental stages; while early reproductive stage is found to be one of the most susceptible phases of a crop to drought stress (Liu et al., 2003). In soybean (*Glycine max* L.), the loss of seed yield is maximal when drought occurs during anthesis (Liu et al., 2003; Liu et al., 2004; Eslami et al., 2010). In a Zimbabwean bambara groundnut landrace, Collinson et al. (1996) reported significant reductions in pod number per plant, harvest index and final seed yield due to terminal drought. Even though drought stress in general negatively affects crop growth and development, inter-and intra-species differences are frequently observed (Leport et al., 1999; Baigorri et al., 1999; Collino et al., 2000; Liu and Stützel, 2002a; Liu and Stützel, 2002b; Mwale et al., 2007). This provides the potential for selecting landraces or cultivars that are suitable for drought-prone regions. To explore the genotypic diversity of crop plants to drought stress, crop physiologists have identified a wide range of physiological and biochemical traits that contributes to drought resistance (Turner et al., 2001). In bambara groundnut, for instance, drought resistance has been ascribed to its ability to maintain leaf turgor pressure through a combination of osmotic adjustment, reduction in leaf area and effective stomatal regulation (Collinson et al., 1997). And in wheat (*Triticum aestivum* L.) and amaranth (*Amaranthus* spp.), it has been found that genotypes with a high capacity for osmotic adjustment could achieve higher yields than those with a low capacity for osmotic adjustment (Blum et al., 1999; Liu and Stützel, 2002a). However, Turner et al. (2007) pinpointed that much of the crop physiology studies have focused on the processes and mechanisms and with less contribution in understanding their relations to the final crop yield; for example, osmotic adjustment did not effect on seed yield under water deficit in chickpea. Alternatively, Turner et al. (2001) proposed a ‘Yield Component Framework’ for selection of high yielding legumes genotypes in consideration of traits affecting crop growth rate, transpiration, transpiration efficiency, and harvest index. Such a framework enables crop scientists to identify the components that link directly to the yield under drought stress conditions.

In this study, intermittent drought stress during anthesis/early reproductive stage was imposed in four bambara groundnut landraces collected from different regions across Africa and East-Asia. The responses of stomatal conductance and transpiration to progressive soil drying and the consequent effects of the drought spell on plant biomass, seed yield and yield components at final harvest were investigated. Our objective was to examine if the immediate physiological responses to soil water deficits vary among the landraces and if that may account for the reduction of the final seed yield.

Materials and Methods

A pot experiment was conducted at the experimental station of the Department of Agriculture and Ecology, Faculty of Life Sciences, University of Copenhagen from 29th May to 27th October 2009. The pot used in the experiment had a volume of 4 liters. The pots were filled with 455 g (dry weight) peat material (Sphagnum, 32% organic matter, pH=5.6-6.4 and EC=0.45 mS cm^{-1}). The photoperiod was 12 h throughout the experimental period and it was controlled by a black polythene screen that was automatic pulled on and off (7:00-19:00 h). Supplementary light on each table consisted of 3 lamps, 400 W each, giving an average photosynthetic active radiation (PAR) of 170 μmol m^{-2} s^{-1} at the top of the canopy. When the ambient light intensity was lower than ca. 75 μmol m^{-2} s^{-1}, the lamps were witched on. In the greenhouse, the air temperature was controlled at 26-30/22-25 °C day/night and the relative air humidity was 30-50%.

Plant material consisted of four bambara landraces of different origin. S19-3 was collected from the dry areas of Namibia with a annual rainfall of 365 mm, Uniswa Red (hereafter referred to as Uniswa) came from Swaziland with an annual rainfall of 1390 mm, LunT was collected from Sierre Leone with an annual rainfall of 4433 mm, and Ramayana was from Bogor in the West part of Java, Indonesia with an annual rainfall of 3337-3655 mm. Two seeds were sowed in each pot on 29th May 2009. Two weeks after sowing, the seedlings were thinned to one plant per pot. The landraces S19-3 and Uniswa had been through two cycles of purification, by single plant selection, and therefore represented third generation inbred material. LunT and Ramayana were bulk material multiplied from the original seed source.

Pots were automatically fully irrigated until 12th August 2009 (75 days after sowing). The irrigation water (Brøste-Pioner, blue), contained full nutrients (pH 5.5; EC-value 1.4; NPK: 14-3-23 (10.7% NO_3^-+3.8% NH_4^+) plus Mg and full micronutrients + Fe (Pioner Micro) to minimize growth variations in the landraces. On 13th August, half of the plants were well-watered (WW) to 2100 gram representing 90% of pot holding capacity (PHC), while the other half were drought-stressed (DS) by withholding irrigation from the pots. The treatments were imposed until the transpiration rate of the DS plants reached 10% of the WW plants (Davatgar et al., 2009).

After onset of the treatments, the pots were weighed daily at ca 9:00 h to calculate the daily transpiration and the soil water status. Soil water status in the pot was expressed as the fraction of transpirable soil water (FTSW). Total transpirable soil water (TTSW) was the difference between pot weight at 100% PHC (with a pot weight of 2300 g) and when transpiration rate of the DS plants decreased to 10% of the WW plants (pot weight ca. 900 g). The daily value of FTSW was estimated by the ratio between the amount of transpirable soil water remaining in the pot and TTSW:

$$FTSW = (WT_n-WT_f)/TTSW \quad (1)$$

Where WT_n is actual pot weight on a given date and WT_f is pot weight at the time when the transpiration rate of the DS plants was 10% of the WW plants. This was taken 9 days after imposition of the stress. After onset of the treatments, stomatal conductance (g_s) on only the abaxial side of the leaf (as the g_s of the adaxial side of the leaf was very low) was measured daily (except the last day) from 10:30 to 12:00 h using a leaf porometer (Decagon Devices Ltd., USA). The measurement was done on two fully expanded leaves at similar developmental stage of each plant, and with four plants per treatment.

To minimize day-to-day variation, the daily values of transpiration rate and g_s of the DS plants were expressed relative to the WW plants, yielding relative transpiration rate and relative g_s. The relationships of relative transpiration rate and relative g_s to FTSW were evaluated using a linear-plateau model (Liu and Stützel, 2002b):

$$\text{Relative transpiration rate or relative } g_s = 1 \qquad \text{if } C_i \leq \text{FTSW} \leq 1; \qquad (2a)$$

$$\text{Relative transpiration rate or relative } g_s = 1 + A \times (\text{FTSW} - C_i) \qquad \text{if FTSW} \leq C_i \qquad (2b)$$

Where A is the slope of the linear equation (2b) and C_i is the threshold of FTSW at which the relative transpiration rate and relative g_s started to diverge, i.e. decline from 1.

All the DS plants were re-watered to the level of the WW plants after the treatment period. The plants were grown under WW condition until physiological maturity of the pods, i.e. 26th October 2009. All plants were then harvested and the shoot dry weight (DW) and seed dry weight (DW) were recorded after drying in an oven at 70 °C for 48 hrs. Seed number per plant and individual seed weight as well as harvest index were also determined.

The experiment was arranged in a completely randomized design with 12 replications. Data were subjected to analysis of variance (ANOVA) procedures (SAS 8.02, Cary, NC, USA). To estimate the A and C_i in the linear-plateau model (Equal 2a and 2b), PROC NLIN of PC SAS (SAS 8.02, Cary, NC, USA) was employed. Coefficient of determination (r^2) was calculated for each regression as 1-SSE/CSS where SSE is the residual sum of squares and CSS is the corrected total sum of squares. Standard errors of the means (SE) were calculated. Paired T-test and Tukey's Studentised Range (HSD) Test were used to detect the statistical differences between the two water treatments as well as between the four landraces.

Results

The soil water status, expressed as the fraction of transpirable soil water (FTSW), declined in a similar pattern for the four landraces in the DS pots until all the transpirable soil water was depleted. By the end of the DS treatment, FTSW was higher for Ramayana than the other landraces (Figure 1). During this period, FTSW in the WW pots was kept at 0.85-0.9 for all landraces (data not shown).

Plant water use during the treatment period is shown in Figure 2. Among the four landraces, S19-3 used the largest amount of water, and LunT used the smallest amount of water under WW condition; under DS, Ramayana had the lowest water use as compared with other landraces.

In the WW plants, S19-3 and Uniswa had higher daily transpiration rate than LunT and Ramayana (Figure 3 A-D). Except for LunT, drought immediately decreased plant transpiration on the second day after withholding irrigation. Despite these differences, the relationship between the relative transpiration rates plotted against the FTSW were similar for all the four landraces. The FTSW threshold, at which the relative transpiration rate started to decline from 1, was 0.73 (Figure 4A). Similar to the transpiration rate, g_s of LunT and Ramayana, was generally lower than g_s of S19-3 and Uniswa under WW condition (Figure 3 E-H). Compared to the WW plants, g_s decreased in the DS plants within 1-2 days after withholding irrigation from the pots for all landraces. In addition, a common relationship between the relative g_s and FTSW was observed over the four landraces, and the FTSW threshold at which the relative g_s become less than 1 was 0.7 (Figure 4B).

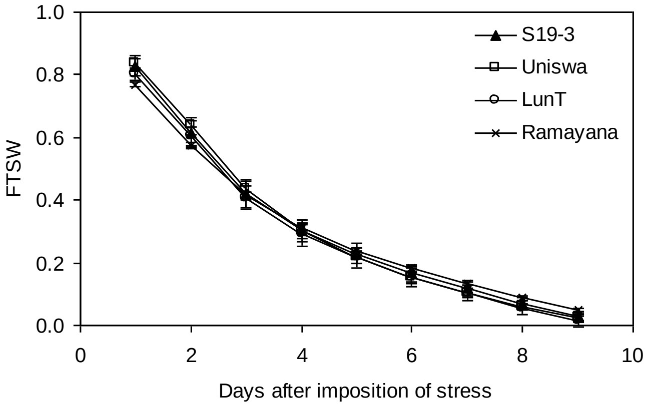

Figure 1. Trends of the fraction of transpirable soil water (FTSW) in the pots of four landraces of bambara groundnut during progressive soil drying. Each data point represents the average of 12 pots. Error bars indicate standard error of the means (SE).

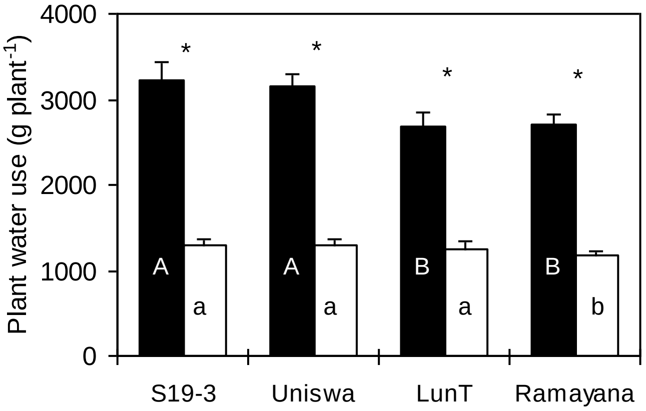

Figure 2. Cumulative plant water use of four landraces of bambara groundnut under well-watered (WW) and drought-stressed (DS) conditions at early reproductive stage. Error bars indicate SE (n=12). The star on the top of the two columns for each landrace indicate significant difference between the water treatments ($P<0.05$) (Paired T-test). The different capital letters on the columns indicate significant differences ($P<0.05$) between the four landraces under well-watered (WW) condition; while the different small letters on the columns indicate significant differences ($P<0.05$) between the four landraces under drought-stressed (DS) condition (Tukey's Studentised Range (HSD) Test).

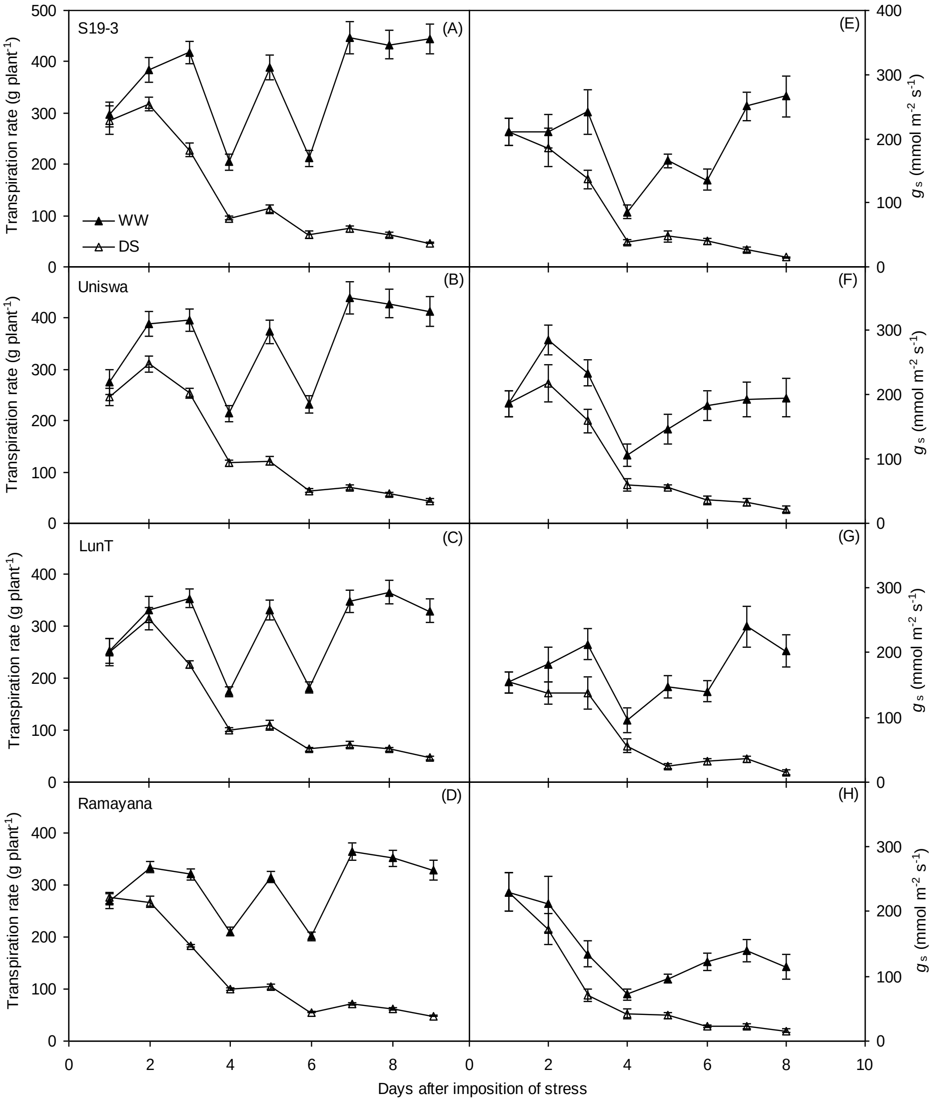

Figure 3. Transpiration rate (A, B, C, D) and stomatal conductance (g_s) (E, F, G, H) of four landraces of bambara groundnut under well-watered (WW) and drought-stressed (DS) conditions at early reproductive stage. Error bars indicate SE (n=12).

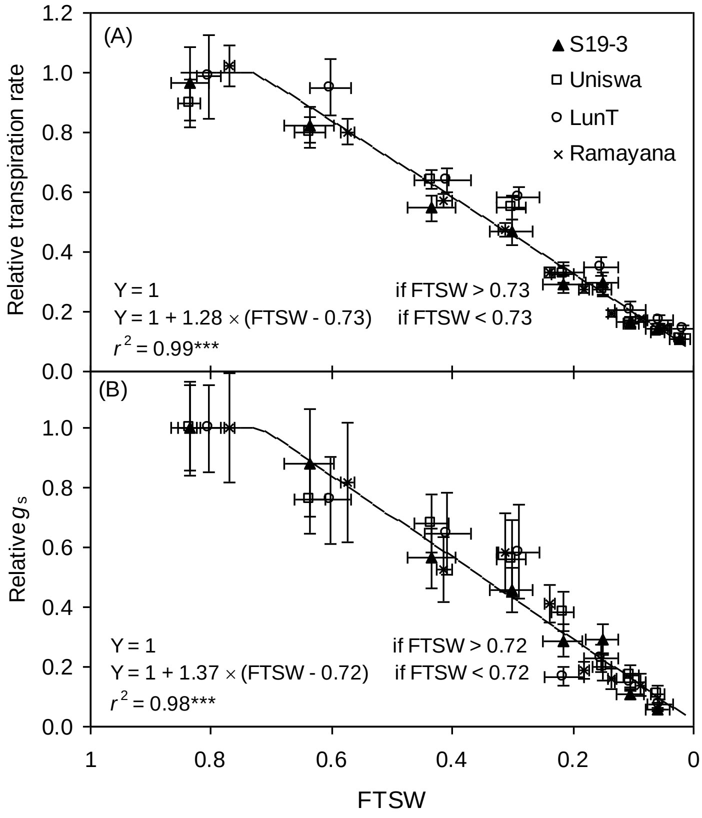

Figure 4. Relationships of relative transpiration rate (A) and relative stomatal conductance (g_s) (B) to the fraction of transpirable soil water (FTSW) in four landraces of bambara groundnuts exposed to progressive soil drying at early reproductive stages. Error bars indicate SE (n=12). As the relationships were similar for the four landraces, therefore the pooled data of the landraces were used to make the linear-plateau regression lines. *** indicates the regression was significant at P<0.001 level.

At the final harvest, the shoot dry weight (DW) of the WW plants was highest for Ramayana and lowest for LunT, and this pattern was found also for the DS plants (Figure 5A). Figure 5A also shows that only for Ramayana the shoot DW was significantly decreased by DS, and DS did not significantly decrease shoot DW in the other three landraces.

Seed dry weight (DW) of the WW plants was similar for S19-3 (25.9 g plant^{-1}) and Uniswa (23.3 g plant^{-1}), which were significantly higher than those of LunT (10.5 g plant^{-1}) and Ramayana (9.1 g plant^{-1}) (Figure 5B). For all landraces seed DW was significantly reduced by drought, and the reduction was the greatest for Ramayana (75%), followed by LunT (68%) and S19-3 (52%), and the smallest for Uniswa (31%) (P<0.001). Under DS, Uniswa had the highest seed DW (16 g plant^{-1}), and intermediate for S19-3 (12 g plant^{-1}), and lowest for LunT (3.4 g plant^{-1}) and Ramayana (2.3 g plant^{-1}). Identically to the seed DW, the same patterns of changes were found in seed number per plant of the four landraces under WW and DS treatments (Figure 5C).

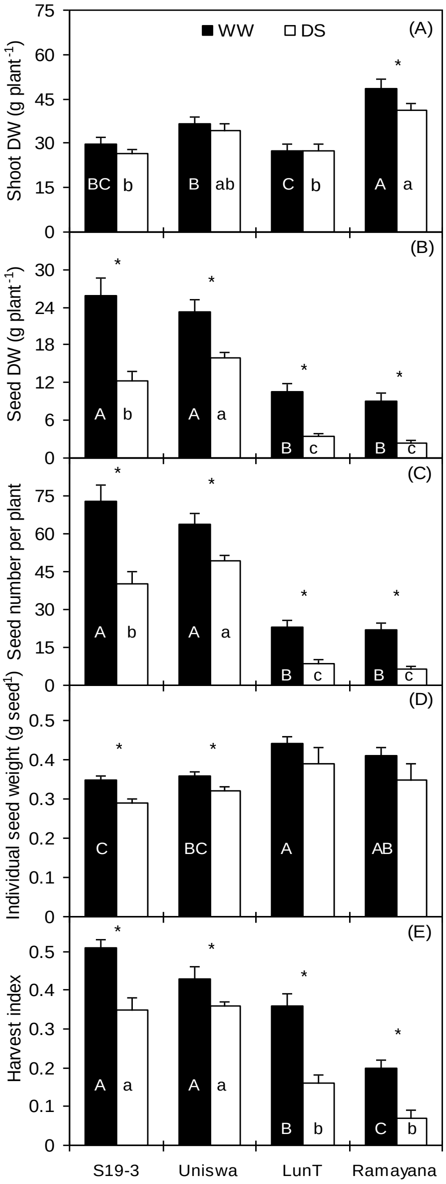

Figure 5. Effects of intermittent drought stress on shoot dry weight (DW) (A), seed dry weight (DW) (B), seed number per plant (C), individual seed weight (D), and harvest index (E) of four landraces of bambara groundnut at final harvest. Error bars indicate SE (n=12). The star on the top of the two columns for each landrace indicate significant difference between the water treatments ($P<0.05$) (Paired T-test); the different capital letters on the columns indicate significant differences ($P<0.05$) between the four landraces under well-watered (WW) condition; while the different small letters on the columns indicate significant differences ($P<0.05$) between the four landraces under drought-stressed (DS) condition (Tukey's Studentised Range (HSD) Test).

Among the four landraces, LunT had the biggest seed size in term of individual seed weight, whereas S19-3 had the smallest individual seed weight. DS only significantly reduced individual seed weight for S19-3 and Uniswa and not for LunT and Ramayana (Figure 5D). There was no interaction between landrace and water treatment on seed size (P=0.96).

Figure 5E shows the harvest index of the four landraces under WW and DS treatments. Under WW treatment, the harvest indexes were similar for S19-3 and Uniswa, which were significantly higher than that recorded for LunT and Ramayana. DS reduced the harvest indexes for all landraces, while the reductions were more pronounced for LunT and Ramayana than for Uniswa and S19-3 ($P<0.001$).

Discussion

The transpiration rate and the total plant water use varied among the landraces under WW treatment (Figures 2 and 3). It is notable that landraces originating from the more wet areas transpired less water than those from the relatively drier areas. The transpiration rate and thus the total plant water use in the WW plants was probably associated with the ontogenetic development of leaf area and with the different g_s of the landraces. Although the leaf area was not determined in the present study, it was noticed during the experiment that Uniswa and Ramayana had bigger leaf area than S19-3 and LunT. Thus, the higher rate of transpiration for S19-3 was probably due to its greater g_s; whereas the bigger leaf area might have contributed to the higher rate of transpiration for Uniswa but not for Ramayana. For LunT, the lower rate of transpiration was possibly a combined result of a small leaf area and a moderate g_s. Under DS, transpiration rate and g_s of all landraces decreased significantly within 1-2 days after withholding irrigation from the pots (Figure 3). Consequently, the total plant water use was reduced by 53-60% across the four landraces during the treatment period (Figure 2).

Despite the variation in the transpiration rate and g_s among landraces, the responses of the two variables to soil drying were similar among the four landraces as indicated by the common relationships of the relative transpiration rate and the relative g_s to FTSW (Figure 4). The FTSW thresholds for reduction of the relative transpiration rate and relative g_s were similar, i.e. ca. 0.7. It is noteworthy that these values are much greater than those reported for other crops (an average FTSW thresholds for transpiration and g_s were 0.3-0.5) (Sadras and Milroy, 1996). One explanation for this difference might be that bambara groundnuts are more sensitive than other crops to soil drying. By closing stomata early in response soil water deficits would conserve water in the soil and allow the plants survival under prolonged drought stress. In addition, the high air temperature (26-30 °C) and low air humidity (30-50%), giving a large vapour pressure deficit (VPD) in the glasshouse during the treatment period, might have contributed to the high FTSW thresholds as indicated by Sadras and Milroy (1996). However, Ray et al. (2002) reported that VPD had no effect on the FTSW thresholds for reduction of transpiration in maize (*Zea mays* L.) hybrids. Besides, Wahbi and Sinclair (2007) reported that, compared with growing plants in the mineral soils, plants grown in peat material reduce their transpiration rates at much higher FTSW values during soil drying. This could partly explain the higher FTSW thresholds observed in this study. Moreover, one may also speculate that the fast soil drying due to the small pot size used in the study might have caused the higher FTSW thresholds. This is seemingly not the case as Ray and Sinclair (1998) reported that pot size had no significant effect on the FTSW thresholds for reduction of transpiration in maize and soybean. Despite of these uncertainties regarding the determination of the FTSW thresholds, the similarity of the response of transpiration and g_s to progressive soil drying implies that the landraces performed similarly in term of stomatal control over water use during the drought spell, and stomatal closure played a central role in reducing plant water use in bambara groundnuts under drought conditions.

Interestingly, although the landraces responded similarly in the stomatal control over water use during the drought spell, the consequent effect of the drought on final seed yield and yield components varied significantly among the four landraces (Figure 5). Even though the shoot biomass was hardly affected by DS treatment for most of the landraces (Figure 5A), the seed yield reduction was more severe for LunT and Ramayana than for S19-3 and Uniswa (Figure 5B). Further, the reduction of seed yield in LunT and Ramayana was due mainly to lowered seed number per plant, as the individual seed weight was unaffected by DS in the two landraces; whereas for S19-3 and Uniswa the reduction of seed yield was ascribed to both a lowered seed number per plant and a decreased individual seed weight (Figure 5 A, C, D). This is in good agreement with earlier findings for other crops such as soybean where DS at anthesis decreased seed number but not seed size, and where the reduction of seed number was mainly ascribed to an enhanced abortion rate of flowers and young pods caused by DS (Liu et al., 2003; Liu et al., 2004).

Although the harvest index was negatively affected by DS for all landraces, LunT and Ramayana were much severely affected than the S19-3 and Uniswa (Figure 5E). It is known that the ability for crop plants to allocate assimilates to the seeds during the post flowing period is a potential source of yield stability under terminal-drought environments (Turner et al., 2001). However, in this study, our results clearly demonstrated that a brief intensive drought spell during early reproductive stage could significantly reduce the harvest index in bambara groundnuts. As the shoot DW was basically not affected by DS, it must have been the sink intensity and not the source capacity that limited final seed yield. This is in accordance with another study where the seed number per plant and not the individual seed weight was reduced under DS (Liu et al., 2005). Moreover, earlier studies in chickpeas have indicated that large seeded varieties are seemingly more vulnerable to DS than small seeded types in terms of seed abortion particularly when DS occurring at early podding stage (Leport et al., 2006). In consistent with this, we observed that LunT and Ramayana had fewer larger seeds than S19-3 and Uniswa Red under WW conditions (Figure 5D), and they were more vulnerable to DS than the latter landraces.

It is notable that only a brief intensive drought spell over 9 days at early reproductive stage had resulted in dramatic reductions in final seed yield for all bambara groundnut landraces. Among the landraces investigated in this study, there was clear genotypic diversity in the performance under DS, being that LunT and Ramayana were more sensitive to drought than S19-3 and Uniswa Red. The different responses of the landraces to DS may reflect their adaptation to the local climates of collection. In our limited collection, landraces from wet regions were more susceptible to drought stress than those from drier regions. However, the physiological responses observed here during the treatment period with respect to transpiration did not correlate well with the effects of DS on seed yield at the final harvest. Therefore, we propose that more investigations on the processes during the early reproductive development like flower and pod abortion, assimilates translocation from source leaves to seeds, and the utilization of assimilates by the developing seeds, are needed to explore the physiological mechanisms for the reduced seed yield under drought in different bambara groundnut landraces. Selection efforts to enhance drought tolerance should focus on these traits.

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