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Reactions of *Adansonia digitata* L. provenances to long-term stress at seedling stage

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Abstract The effects of drought stress on growth parameters and dry matter partitioning of seven provenances (six from West Africa and one from East Africa) of *Adansonia digitata* L. were assessed in a seedling experiment in Burkina Faso. Three water regimes corresponding to 100 % (control), 75 % and 50 % of field capacity were applied over a period of 18 months. While survival was unaffected by the stress treatments, provenances and water regimes significantly affected growth parameters, and plant dry matter accumulation was significantly reduced by water stress. Provenances had growth rates of diameter and height in response to stress. The fresh weight/dry weight ratio increased with increasing stress. In response to stress, shoot/root ratios decreased at the start of the experiment, but increased at the end, compared to the control. Differences between provenances were not correlated to environmental parameters of the site of origin, and the hypothesis about better resistance of seedlings from drier sites to drought stress was not confirmed. However, the provenance from East Africa was in several aspects different from the West African provenances.

Keywords Adaptation · Baobab · Drought tolerance · Relative growth rate · Sahel · Shoot–root ratio

Introduction

Adansonia digitata L. is the most widespread species of the Adansonia genus that comprises eight species (Baum et al. 1998). In Sub-Saharan Africa, the species is regarded as very important because of its non-timber

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forest products (twigs, fruits, seeds, leaves and flowers) which are used as common ingredients in traditional dishes of rural and urban areas (Assogbadjo et al. 2011). Studying the ethnobotanical knowledge on baobab in three ethnic groups (Peulh, Serer and Wolof) in Senegal, Prehsler (2009) listed 502 utilisations of which 47 % are for nutritional purpose, 14 % for medicinal, 3 % for spiritual, 1 % for veterinarian, and 35 % for other uses. Use patterns and use values vary between communities (De Caluwe et al. 2009). There is a huge diversity of knowledge on baobab products in the distribution area of the species.

In addition to the local use of products of *A. digitata*, baobab fruit pulp obtained novel foods approval in 2008 by the European Union, allowing African farmers an opening door for European food industries (Hermann 2009). It has been suggested to put conservation measures (Jama et al. 2008) as well as domestication strategies in place for a better use of the species and thus contribute to a better income and livelihood of African farmers who are nurturing the tree in their farmlands.

The socio-economic importance of the baobab and the concerns about its ability to adapt to changing climate has prompted many studies. *A. digitata* is found in the hot and dry savannahs of sub-Saharan Africa where the availability of water is known to be the predominant limiting factor for the vegetation cover (Junk 2002). Despite the harsh conditions, the species may grow up to 25 m in height and 10 m in trunk diameter (Wickens and Lowe 2008). In its distribution area in West Africa, there are steep gradients of precipitation ranging from south to north (1,600–400 mm), and the species may have adapted to different rainfall regimes (Robertson et al. 2006). Studies of two other Sahelian tree species, *Faidherbia albida* and *Vitellaria paradoxa*, showed differences in water consumption between provenances (Bayala et al. 2009; Roupsard et al. 1998). Climatic envelope modelling suggested a strongly reduced distribution area of *A. digitata* in the future as a result of climate change (Cuni Sanchez et al. 2011). If the species has adapted to prevailing rainfall conditions, understanding adaptation patterns may help develop better strategies for use, domestication and conservation of its genetic resources.

Studies of fruit, leaf and tree characters in natural populations have demonstrated clinal variation in several traits. Often this variation was correlated with differences in annual precipitation between sites (e.g. Cuni Sanchez et al. 2010; Parkouda et al. 2012; Simbo et al. 2013). That at least some of this variation is due to genetic differences between provenances was demonstrated by Cuni Sanchez et al. (2010) who showed that provenances from Benin differed in their leaf morphology, provenances from areas with low precipitation showing more xerophytic characters than provenances from more humid areas. Likewise, differences in growth rate between provenances were demonstrated in nursery trials by Cuni Sanchez et al. (2011) and Korbo et al. (2012). Especially the clinal variations in characters such as stomatal density and size (believed to be closely coupled to water use of plants) indicate that populations have adapted to the local precipitation patterns. This led us to hypothesise that drought will have a differential impact on the growth of *A. digitata* provenances, and that seedlings from drier areas will show better resistance to drought stress by higher survival and growth.

So far, there is only one report on provenance differences in drought response. De Smedt et al. (2012) compared provenances from Mali and Malawi in a short stress trial. While there were significant differences in drought stress responses between provenances from the two countries, there were no significant differences between provenances within the countries, despite the provenances being sampled across gradients in rainfall. In this paper we study a different set of provenances, sampled across a rainfall gradient, subjected to long term water stress. We intend to show that provenances react differently to drought stress with respect to growth, dry matter production and partitioning of seedlings, and if proven, we will investigate whether this variation can be related to precipitation at their origins. In a closely related paper, we will investigate anatomical and physiological consequences of the stress on the same provenances (Bouda et al. in preparation).

Materials and methods

Study site, substrate and plant material

The experiment was carried out in the nursery of the Centre National de la Recherche Scientifique et Technologique (CNSRT) in Ouagadougou, Burkina Faso (1°12′13.9W, 11°33′24.6″N, 306 m a.s.l.). The rainy season is from May to October, with the main quantity of water falling between June and September. The average annual precipitation of the 20 last years is

Table 1 Geographic position and climate of the origin of seven provenances of *Adansonia digitata*

Provenance	Country	Latitude	Longitude	Altitude (m)	Rainfall (mm year^{-1})	Temperature average (°C)
Komodiguili	Mali	14°41′N	03°40′W	587	400	26.4
Liptougou	Burkina	13°10′N	00°19′E	240	550	28.5
Samé	Mali	14°20′N	11°39′W	45	600	29.0
Kolangal	Burkina	12°57′N	00°56′E	240	620	28.5
Nobéré	Burkina	11°33′N	01°12′W	300	800	28.0
Koumadiobo	Mali	11°51′N	06°93′W	305	1,100	27.3
MKundi	Tanzania	10°57′S	39°34′E	260	1,525	23.5

Precipitation and temperatures were obtained from the "New_LocClim_1.10 2005"

804 mm. The temperatures vary between 16 °C (December–January) and 43 °C (April–May). The average monthly air humidity ranges between 23 % (dry season) and 80 % (rainy season) (MECV/BF 2007).

The plant material was composed of seeds from seven provenances. Six were from West Africa (Kolangal, Liptougou and Nobéré in Burkina Faso, Komodiguili, Koumadiobo and Samé in Mali) and cover the different agro-climatic zones of *A. digitata* distribution in the Sahel region. One provenance from Mkundi in Tanzania was selected as a representative of the eastern part of its distribution area. Details of seed collection sites are given in Table 1.

To break their dormancy and increase germination, the seeds were pre-treated by soaking them in 95 % sulfuric acid for 45 min, then in water for 24 h. Seeds were then sown on October 22, 2008, directly into 630 cylinder aluminium pots (diameter 10 cm x 50 cm height), containing 6.5 kg of substrate consisting of 50 % of forest soil, 25 % manure and 25 % sand. The analysis of the substrate in the laboratory gave the following composition: 8 % clay, 7 % silt, 12 % fine sand, 62 % coarse sand and 10 % $CaCO_3$. The mixture had a pH of 8 in 1.0 M KCl, and contained 1 % total C and 0.06 % total N. Each pot received 7 seeds. Nine other pots with the same substrate were kept without seeds to serve as control of water loss by evaporation. Two weeks after sowing the germination was completed in all pots. On November 5th, 2008, the plants were thinned leaving only one plant per pot. After emergence, all pots received the same quantity of water every three days until the stress treatments started on February 4th, 2009. The plants were covered by a transparent plastic roof to avoid uncontrolled water without blocking the sun light.

Stress treatments and experimental design

The applied quantities of water were calculated based on soil water content at field capacity (Ward and Robinson 1990). The field capacity was estimated by measuring the amount of water held in the soil. Nine pots with dry substrate (dried at 60 °C for 72 h) were weighed (W1). The pots were thoroughly watered and let to drain for 48 h before the pots were weighed again (W2). The difference W2 − W1 corresponds to the amount of water that should be added to a completely dry substrate to reach 100 % field capacity. Three water regimes were applied: Irrigation to 100, 75 and 50 % of soil field capacity referred to in the text as high water content (HWC), medium water content (MWC) and low water content (LWC), respectively. Assessed at the end of the experiment, predawn water potential of plants in the LWC treatment varied from ca. −0.82 MPa the day after watering to −1.08 MPa seven days after watering. The stress experiment lasted eighteen months. Every 7 days, the pots were weighed and watered up to the water level of the regime for each pot. Increases in seedling weight were estimated based on a regression of the relationship between seedling fresh weight (Y in g) and seedling root collar diameter (X in mm), determined in a separate experiment (Bouda, unpublished data):

$$Y = 0.223X^2 + 14.271X + 661.285 \left(R^2 = 0.75\right) \tag{1}$$

The experiment was a split plot design with provenance as the main plot and water regime as the sub-plot, replicated three times. Each sub-plot had ten plants. Each of the three blocks contained 7 provenances × 3 water regimes × 10 plants, giving a total of 630 plants for the whole experiment.

Data collection and statistical analysis

Survival rate, root collar diameter and seedling height were recorded zero, six, twelve and eighteen months after the beginning of the stress (the time 0 corresponded to 3 months after sowing). In August 2009, after six months of stress, one third of the pots were randomly chosen within each subplot (210 pots in total), and the living seedlings (183 seedlings, corresponding to 87 % survival) were uprooted for dry matter and root assessments. After twelve months of stress, in February 2010, the second third of the seedlings were uprooted and assessed (173 seedlings, 82 % survival), and after eighteen months of stress (August 2010) the remaining living seedlings were harvested (169 seedlings, 80 % survival). The variation in the numbers of seedlings uprooted at each date is due to mortality.

At each harvest, the assessments included seedling height, diameter at root collar, fresh and dry weight of root and stems. The following abbreviations will be used subsequently: TFW (total fresh weight), TDW (total dry weight), SDW (shoot dry weight) and RDW (root dry weight). The ratios TFW/TDW and SDW/RDW were calculated.

The mean relative growth rate (RGR) was calculated for diameter (at six, twelve and eighteen months). The RGR may be used to compare the growth of seedlings that differ in initial size in order to neglect the growth differences due to the size, as was the case in our study (Hunt 1982). RGR was calculated based on the mean values obtained from two adjacent periods as:

$$RGR_A = \frac{\ln A_F - \ln A_I}{t_F - t_I}, \tag{2}$$

where A_F denoted the measured trait at the end of the period, A_I denoted it at the start of the period (in this case at month 0 of stress or 3 months after sowing) and $t_F - t_I$ was the length of the period in weeks.

In cases where RGR is calculated based on harvest of several individuals (TDW in this case), the above formula has bias that was avoided by using another formula (Hoffmann and Porter 2002):

$$RGR_A = \frac{\overline{\ln A_F} - \overline{\ln A_I}}{t_F - t_I}, \tag{3}$$

where $\overline{\ln A_F}$ and $\overline{\ln A_I}$ are the means of the logarithm-transformed plant weights.

The RGR of diameter, height and total dry weight are referred to as $\mathrm{RGR_d}$, $\mathrm{RGR_h}$, $\mathrm{RGR_{tdm}}$ respectively.

Before statistical analysis, mean values for all parameters in each subplot were calculated. All—variables (survival, diameter, height, TDW, TFW/TDW, SDW/RDW) were subjected to repeated measures analyses using linear normal models (proc GLM, SAS institute Inc.), including the effects of provenance, water regime, time and the interactions between these factors. For the two ratios, logarithmic transformations were necessary to obtain residuals following normal distributions. Estimates based on data transformed for analysis (log) were back-transformed to give the geometric mean values.

Before removal of non-significant effects (at the 5 % level), the model used for all variables was:

$$Y_{IJKZ} = B_I + P_J + R_K + T_Z + PR_{JK} + PT_{JZ} + RT_{KZ} + BP_{IJ} + P_J R_K T_Z + \varepsilon_{IJKZ}, \tag{4}$$

where Y_{IJKZ} was the response variable, B_I was the effect of block, P_J the effect of provenance, R_K the effect of water regime, T_Z the effect of time and PR_{JK}, PT_{JZ}, RT_{KZ} and $P_J R_K T_Z$ were the interactions between provenance and water regime, provenance and time, water regime and time, and the three way interaction between provenance, water regime and time respectively. BP_{IJ}, the interaction between block and provenance, was the random effect, included to account for the split-plot design. ε_{IJKZ} represented the residuals, assumed to be independent and following normal distributions $N(0, \sigma_e)$. Though non-significant effects were removed sequentially, we always kept PR_{JK} in the model because of our special interest in the differences in reaction between provenances. Since some seedlings died during the experiment, the analysis includes only seedlings that were alive at time of data collection.

The results of analysis were validated by inspecting the residuals and quantile–quantile plots (Clewer and Scarisbrick 2001). The mean values presented are least square means.

Because the provenance Mkundi was the only representative from East Africa, we investigated how this provenance affected the results by running the analyses with and without the provenance. A contrast of interest analysis was included, comparing the Mkundi provenance to the mean value of the rest of

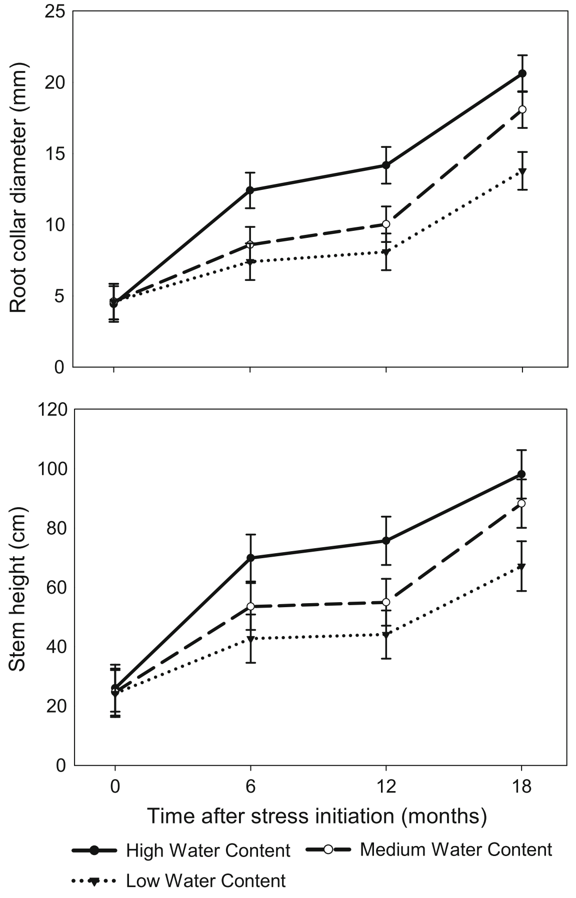

Fig. 1 Average effect of water regime on root collar diameter and stem height of *Adansonia digitata* seedlings. *Error bars* denote upper and lower 95 % confidence intervals ($n = 3$)

the provenances by assigning a weight of −1 to Mkundi and 1/6 to the rest of the provenances.

Results

Survival

While the survival of West African provenances varied between 85 % (Nobéré) and 98 % (Samé and Koumadiobo) across the three periods and did not vary significantly from each other, Mkundi had a significantly lower survival of only 32 %. Water regime had no effect on survival, and there was no interaction between provenance and water stress treatment at any of the measurement dates (indicating that the provenances reacted similarly to the stress). The major part of the mortality took place in the first six months after initiation of the water stress treatments, and the average survival of the trial was 87, 82 and 80 % after six, twelve and eighteen months of stress, respectively. For the same periods, the survival of seedlings from Mkundi was 32, 32 and 33 % respectively, and the contrast of interest analysis showed that Mkundi differed significantly from the West African provenances ($P < 0.0001$).

Diameter and height

The growth was fast in the period February–August, slow from August-February and then increased again during the last period from February–August (Fig. 1). Water regime had highly significant effects on growth parameters (root collar diameter and height). Diameter and height were significantly reduced under the MWC and LWC water regimes compared to the seedlings in the HWC regime (Fig. 1). This was also the case for relative growth of diameter (Fig. 2). Differences in relative growth rate between treatments were largest after 6 months and then became smaller.

Provenance effects were not significant, and there were no significant interactions between provenance and water regime for height and collar diameter. However, the interaction between provenance and water regime was significant for the relative growth rate of diameter ($P < 0.0001$). In particular the relative growth rates for MKundi were much influenced by the stress treatments. This interaction was also significant when MKundi was excluded, and Kolangal and Komodiguili appeared to be among the sensitive provenances, while less responsive provenances were Samé, Nobéré and Koumadiobo. The data did not show any correlation between the growth of provenances and the climatic and geographical parameters of their origins.

Dry matter

Significant effects of water regime on the plant dry matter was observed at all harvesting dates ($P < 0.0001$). The stress treatments reduced the plant dry matter accumulation (Table 2). There were no significant differences between provenances, and no significant interaction between provenance and water regime was detected, again indicating that the provenances responded in a similar manner to drought. While the amount of dry matter per plant increased

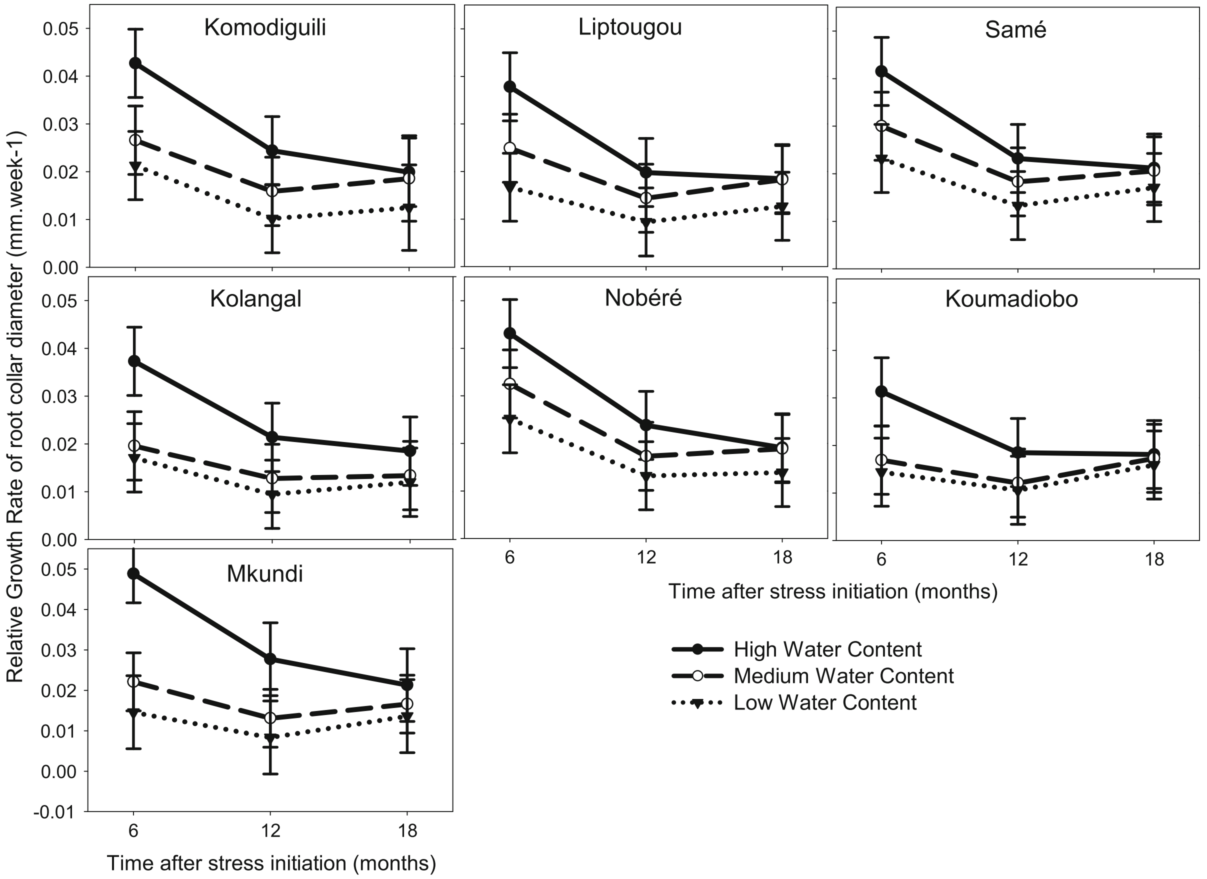

Fig. 2 Effects of provenance and water regime on relative growth rate of root collar diameter of *Adansonia digitata* seedlings. *Error bars* denote upper and lower 95 % confidence intervals ($n = 3$)

throughout the experiment in the HWC regime, it decreased from month 6 to month 12 in the MWC and LWC regimes and then increased again. At least part of the decrease in dry weight from month 6 to 12 is due to shedding of leaves during the cold season.

Water content and dry matter partitioning

Provenance and water regime had significant impacts on both TFW/TDW and SDW/RDW at all assessments (Table 2), but interactions between provenance and water regime were not significant. The TFW/TDW ratio increased with increasing severity of stress at all assessments (Table 2), and was largest after twelve months of stress. At the provenance level, Komodiguili, Samé and Komadiobo displayed high ratios after six months of stress, while Mkundi had the lowest value, meaning that Mkundi had less fresh weight per g of dry weight than the other provenances. Mkundi maintained a low value at 12 and 18 months, but at 12 months differences between the other provenances were small, and at 18 months differences between Mkundi and the other provenances had narrowed down, leaving Komadiobo with the lowest value (Table 2). The contrast of interest analyses confirmed that Mkundi was highly significantly different from the West African provenances, but only at 6 and 12 months whereas at 18 months differences were non-significant.

At six and twelve months after stress, the ratio between shoot and root dry matter, SDW/RDW, was high in the HWC treatment, intermediate in the MWC treatment and low in the LWC treatment. It decreased after twelve months of experiment in all water regimes. However, after eighteen months of stress, the tendency was reversed, SDW/RDW now being

Table 2 Biomass (dry weight) accumulation and partitioning in provenances of *Adansonia digitata* under three water regimes

Time after stress initiation	6 months			12 months			18 months		
Variable	TDW (g)	TFW/TDW	SDW/RDW	TDW (g)	TFW/TDW	SDW/RDW	TDW (g)	TFW/TDW	SDW/RDW
Provenance									
Komodiguili	15.2 ± 2.3	9.5 ± 0.4a	1.1 ± 0.1b	11.2 ± 1.2	11.7 ± 0.7a	0.9 ± 0.1ba	38.7 ± 3.5	7.9 ± 0.4ba	1.9 ± 0.2b
Liptougou	16.7 ± 2.3	8.8 ± 0.3b	1.0 ± 0.1bc	13.6 ± 1.2	11.2 ± 0.7ba	0.8 ± 0.1b	37.9 ± 3.0	7.7 ± 0.4ba	1.9 ± 0.2b
Samé	15.1 ± 2.3	10.0 ± 0.4a	1.0 ± 0.1bc	16.0 ± 1.2	10.5 ± 0.7bac	0.6 ± 0.1c	41.2 ± 3.0	8.5 ± 0.4a	1.7 ± 0.2c
Kolangal	14.1 ± 2.3	8.7 ± 0.3bc	0.8 ± 0.1c	10.7 ± 1.2	11.3 ± 0.7ba	0.7 ± 0.1bc	35.6 ± 3.0	8.5 ± 0.4a	1.8 ± 0.2b
Nobéré	16.7 ± 2.3	8.0 ± 0.3c	1.1 ± 0.1b	14.2 ± 1.2	10.1 ± 0.6bc	1.0 ± 0.1ba	40.7 ± 3.0	7.6 ± 0.4ba	2.0 ± 0.2b
Koumadiobo	15.6 ± 2.3	9.5 ± 0.4a	1.5 ± 0.1ba	12.8 ± 1.2	11.8 ± 0.7a	0.9 ± 0.1ba	45.7 ± 3.0	6.9 ± 0.3c	2.0 ± 0.2b
Mkundi	11.3 ± 2.3	6.8 ± 0.6d	1.7 ± 0.3a	8.1 ± 1.7	7.7 ± 0.7c	1.6 ± 0.2a	38.7 ± 3.5	7.2 ± 0.4b	2.2 ± 0.3a
P value	0.9838	0.0307	0.0129	0.1097	<0.0001	<0.0001	0.1315	0.0006	0.2195
Treatment									
HWC	21.0 ± 0.8a	7.7 ± 0.03b	1.3 ± 0.1a	25.3 ± 1.8a	9.5 ± 0.4b	1.0 ± 0.07a	59.5 ± 2.0a	6.7 ± 0.2c	1.4 ± 0.1b
MWC	11.3 ± 1.8b	9.0 ± 0.04a	1.2 ± 0.1a	9.6 ± 0.8b	11.1 ± 0.5a	0.9 ± 0.06a	38.7 ± 2.0b	7.7 ± 0.2b	2.1 ± 0.1a
LWC	8.3 ± 1.8c	9.6 ± 0.04a	1.0 ± 0.1b	6.5 ± 0.8c	11.1 ± 0.5a	0.8 ± 0.05b	21.2 ± 2.1c	8.9 ± 0.3a	2.4 ± 0.2a
P value	<0.0001	<0.0001	0.0006	<0.0001	0.0036	0.0372	<0.0001	<0.0001	<0.0001

Values are means ± standard errors. Provenance and treatment values followed by the same letter within a column are not significantly different at $P < 0.05$ (Tukey's test)

TDW Total dry weight, *TFW/TDW* ratio total fresh to total dry weight, *SDW/RDW* ratio shoot to root dry weight highest in the LWC treatment and lowest in the HWC treatment. Likewise, the SDW/RDW increased compared to the ratios after six and twelve months (Table 2). At provenance level, Mkundi always showed the highest ratio and was distinctly different from the rest of the provenances. Again this was confirmed by the contrast of interest procedure, finding highly significant differences between Mkundi and the West African provenances at 6 and 12 months, but not at 18 months. The lowest values were displayed by Kolangal after six months of stress and Samé after twelve and eighteen months of stress.

Discussion and conclusion

Drought stress response of baobab

A. digitata is generally described as a drought resistant species with an outstanding ability to withstand severe drought and fire (Cuni Sanchez et al. 2010). For example, the species was found at sites with a precipitation of less than 100 mm per year and less than 3 months rainy season in Northern Africa (Wickens 1983). Our experiment confirms this as survival was not affected by the drought stress, and all provenances except Mkundi had a high survival rate (≥80 %). In a similar trial, *Parkia biglobosa* demonstrated extreme sensitivity to drought stress as survival was almost zero in the MWC and LWC treatments after 18 months (Bouda et al. 2013).

Water content in fresh baobab wood was high compared to *P. biglobosa* (Bouda et al. 2013). The fibrous wood of baobab has a high proportion of water-storing parenchyma cells (Wickens and Lowe 2008). Even though this has been hypothesised to make the plants relatively independent of water and allow the baobab some plasticity during periods of water deficit, evidence from Malagasy baobabs suggested that the stored water does not maintain photosynthesis during water deficits. Data instead indicated that water was used for expansion of leaves during flushing in the dry season, and that it played a crucial role in the architecture of the species (Chapotin et al. 2006a, b). Still, mature baobabs undergo significant fluctuations in girth diameter, associated with presence or absence of precipitation (Chapotin et al. 2006a; Fenner 1980). Even though the low conductance from parenchyma tissues to conducting tissues may limit the availability of stored water for photosynthesising tissues, it seems likely that water in the stem may provide some buffering capacity when water potentials in leaves are low (Meinzer et al. 2009). The periodic watering applied in our experiment could thus fit the baobab well, allowing replenishing of water in roots and stems after watering, followed by a slow release of water to the leaves. The ratio between fresh and dry weight showed that water stressed plants accumulated relatively more water than plants in the control treatment, indicating that water storage was enhanced in stressed plants. Following the arguments of Chapotin et al. (2006a, b) this would indicate a better ability to withstand the long dry period and still be able to flush at or before the start of the rainy season.

Another mechanism rendering baobabs drought tolerant may be a strongly regulated transpiration. Comparing the water loss from abscised twigs, Fenner (1980) found that *A. digitata* has better control of water loss than any of the eight other dryland species studied from the same area in Kenya. This was despite baobabs having less sclerophyllous leaves than many of the other species. Chapotin et al. (2006a, b) found that water use in Malagasy baobabs was highly regulated and transpiration limited to periods when water was readily available in the soils. The strong stomatal regulation of transpiration in *A. digitata* was confirmed by De Smedt et al. (2012), suggesting that baobab is an isohydric species. According to Van den Bilcke et al. (2013), the drought avoidance and conservative water use of baobab could be due to the tight control of stomatal closure and rapid leaf loss caused by a brief period of water stress. At the end of the trial, seedlings in the low water treatment had a biomass only a third of seedlings in the control treatment (Table 2). A high survival rate coupled with marked growth responses would be expected in species with efficient regulation of water transport, as long as the drought does not lead to carbon starvation and subsequent death (McDowell et al. 2008). The decrease in dry weight from month 6 to 12 in the stress treatments could be due to carbon starvation, but must also at least in part be attributed to leaf shedding in these treatments. Leaf loss in some cases started two weeks after initiation of the stress treatments.

Despite the fact that water treatments were the same throughout, there were significant time effects on growth. Height and diameter growth was slow from month 6 to month 12, and then increased to month 18. The period with slow growth coincides with the cold and dry period where baobabs in the Sahelian environment would normally be at rest without leaves. Similarly, Korbo et al. (2013) found low production of leaves in the cold and dry season in an irrigation experiment in Mali.

The allocation of biomass to root and shoot is dynamic as demonstrated by Cuni Sanchez et al. (2011) on seedlings of baobab from 3 to 18 weeks of age. It is frequently observed that water stress lead to increased investments in root biomass compared to shoot biomass, thus increasing the ability to take up water (Aref and El-Juhany 1999). Besides, the tap roots of baobab seedlings are tuber-like and store large amount of water (Van den Bilcke 2014). However, our study of the ratios between shoot and root weight showed surprising results. While during the first assessments (at 6 and 12 months after initiation of stress) the shoot/root ratio decreased with increasing stress as was also observed by De Smedt et al. (2012), after 18 months the shoot/root ratio increased and became highest in water stressed plants. It is possible that this shift reflect an ontogenetic change and a corresponding change in strategy: the first year drought stressed seedlings tend to invest more in roots, whereas the second year the strategy changes to invest more in shoots to facilitate carbon capture. This finding merits further studies and underlines that long term drought stress experiments are needed to understand the performance of baobab in the field.

Differences between provenances

Phenotypic variation between baobab populations has been recorded frequently, showing differences in fruit form and size, leaf morphology, tree size, fruit yield and content of various substances, such as vitamins and minerals (Cuni Sanchez et al. 2010; Jensen et al. 2011; Parkouda et al. 2012). As stated in the introduction, these variations were in some cases correlated to climatic and environmental parameters. Genetic marker studies suggest relatively clear differentiation between populations (Kyndt et al. 2009; Pock Tsy et al. 2009). Within the West African populations, Kyndt et al. (2009) using AFLP markers found high levels of structuring between populations. This was suggested to be due to limited gene flow between populations. Finally, using the same markers, Assogbadjo et al. (2006) found genetic structuring within populations in Benin, showing that populations within the same ecological zone were more closely related than populations from different zones. Molecular markers thus showed regional as well as local variations within the species. Given the strong gradients of precipitation in the area that we sampled, it would be expected that genetic structure and limited geneflow would result in locally adapted landraces within the species.

However, the current study only partially confirmed the hypothesis that provenances would react differently to drought stress. We found no significant differences between provenances for height, diameter or biomass, and survival of provenances was significantly different only when the East African provenance Mkundi was included. Only for the relative growth rate of diameter we found significant interactions between treatments and provenances, confirming that provenances reacted differently to drought stress. This indicates that differences in growth response were too small or within-provenance variation too large for most variables to become significant.

Mkundi differed from the West African provenances in several aspects, including the overall shoot/root ratio (the highest) and the survival (the lowest). Mkundi also had the lowest fresh weight to dry weight ratio at the two first assessments. Pock Tsy et al. (2009) found clear distinctions between eastern and western populations of the African baobab using chloroplast markers, and Pettigrew et al. (2012) presented evidence for the segregation of East African baobabs into two species, the tetraploid *A. digitata* and the diploid *A. kilima*. Whereas *A. digitata* was found predominantly at low altitudes, *A. kilima* seemed to be located at elevations above 800 m. Since we have not tested the ploidy of the Mkundi provenance, it is possible that it could belong to the diploid *A. kilima*, but given that Mkundi was collected at an altitude of only 260 m this seems unlikely. It is tempting to attribute Mkundi's performance in our trial to the more general picture differentiation between eastern and western populations. There is an increasing amount of literature showing differences in growth rates between seedlings from East and West Africa, both in nursery studies (Cuni Sanchez et al. 2011; De Smedt et al. 2012) and in a field trial (Korbo et al. 2012).

Considering the West African provenances, there seemed to be no link between growth rate, biomass partitioning and water content, even though the provenances differed in these characters (Table 2). Furthermore, we found no link between geographic origin and climate on the one hand and growth performance and biomass partitioning on the other. For example, the three provenances that were less sensitive to stress (Nobéré, Liptougou and Koumadiobo) vary in average annual precipitation from 550 to 1,100 mm, and Komodiguili from the driest site had a poorer performance under stress. As baobabs are very long-lived plants it cannot be excluded that the populations tested in this experiment have established under climatic conditions different from the current climate (Nicholson 2001). Yet, even if the estimated precipitations in Table 1 reflect the recent decades, earlier precipitation patterns would probably leave the rank of provenances relatively unchanged. Thus, the lack of correlation leaves the door open for speculations. Do we need to stress the provenances even more, to lethal levels of drought, to see their true adaptive potential? Could it be that the populations, because of relative genetic isolation, have evolved along different paths and developed different mechanisms to cope with drought stress? Or are other factors than drought stress more important for adaptation of the populations?

It follows that we are reluctant to give any provenance recommendations for planting based on the results, other than to use extreme caution if provenances from East Africa are introduced to West Africa. Similarly, the lack of correlation between biomass partitioning and performance under stress means that we would not give planting recommendations based on the morphology of the plants. Until a better understanding of baobab physiology under drought stress has been achieved, there seems to be no alternative to long term field testing.

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