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RESEARCH ARTICLE

Variation in baobab (*Adansonia digitata* L.) leaf morphology and its relation to drought tolerance

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Abstract The baobab tree (*Adansonia digitata* L.) is a valued savannah tree. Although variation in fruit characteristics of this tree have been studied, no studies to our knowledge have been carried out on variation of leaf morphology which can be linked to drought adaptation mechanisms. Accessions of baobab from different ecosystems in Benin were characterised for leaf size and thickness, stomata size and density on the abaxial surface of leaves. Significant variation was found in leaf size and stomata characteristics. Trees from northern study sites had higher stomata density and smaller guard cell length than those from southern study sites. The results show that pruning has a significant effect on leaf size, but not on stomatal characteristics. Trees from northern study sites showed more xerophytic characteristics than those from the south. It seems that genetic and physiological effects may play a role in baobab drought adaptation.

Keywords *Adansonia digitata* · Drought · Leaf morphology · Stomatal density · Stomatal size

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Introduction

The baobab tree, *Adansonia digitata* L. (Family Malvaceae), indigenous to tropical Africa, is associated with the drier parts of the savannah (Wickens 1982).

It is characterized by its massive size and for its multiple uses. Tubers, twigs, fruits, seeds, leaves and flowers are all used as common ingredients in traditional dishes of rural and urban areas (Nordeide et al. 1996). Available studies so far indicate that baobab leaf and fruit pulp have high nutritional value in terms of vitamins and minerals (Nordeide et al. 1996; Baobab fruit Company 2003; Phytotrade Africa 2006; Wickens and Lowe 2008). Apart from food, the species supply livestock fodder, fiber for clothing, material for hunting and fishing, shade and medicine for local people (Wickens 1982; Sidibé and Williams 2002). Many of the products are sold in markets and are an important source of income for people (Chicamai et al. 2004; Diop et al. 2005). Due to its importance for non-wood forest products, baobab tree has been identified as one of the most important edible savanna trees to be conserved, domesticated and valorized in West Africa (Eyog Matig et al. 2002). Research efforts, especially in West Africa, have provided relatively recent data on: ethno-botanical knowledge, agronomy, processing techniques, chemical properties, ecology, distribution, propagation and genetic diversity of baobab (Assogbadjo et al. 2005a, b, 2006, 2008, 2009; Chadare et al. 2008; Chia et al. 2008; Diop et al. 2005).

Within the species, *A. digitata*, there is evidence indicating the presence of a number of local types differing in habit, vigour, size, quality of fruits and vitamin content of the leaves (Gebauer et al. 2002; Sidibé and Williams 2002). Assogbadjo et al. (2006) found morphogenetic differences in fruits from one agro-climatic zone to the other in Benin. Abrams et al. (1990) suggested that leaf morphological variation can be linked to drought adaptation mechanisms. It has been reported for *Parkia biglobosa* (Jacq.) G. Don. (a leguminous tree of African savannah) that seedling morphology and leaf anatomy was linked to drought tolerance (Teklehaimanot et al. 1998). However, no studies have been undertaken on baobab leaf size and shape variation.

Drought is one of the main factors limiting growth, development and productivity of plants (Blum 1997). Climate change scenarios predict more severe droughts in the African savannah (Brooks 2004). In order to identify superior sources of planting material, it seems important to identify baobab trees adapted to drought. The aim of this study was therefore to assess baobab trees for drought tolerance by using easily quantifiable leaf morphological characteristics.

Materials and methods

Site selection

In order to assess the variation in baobab leaf morphology and its relation to drought tolerance three experiments were carried out in Benin.

Experiment 1: *in situ assessment of leaf morphological variation*. Observations were made on the morphology of baobab trees maintained in farmed fields, habitations and their boundaries in eight sites in Benin (Table 1; Fig. 1). Study locations were selected following a latitudinal gradient with the main criterion being high tree density (>5 ind/km^2 determined by Assogbadjo et al. 2005b) and accessibility. Ten trees, with 0.5–1.5 m DBH (diameter at breast height) at 100 m apart were randomly selected in each village.

Experiment 2: *ex situ assessment of leaf morphological variation*. Observations were made on 12-month-old trees grown in the experimental farm of the Faculty of Agronomy (FSA) in the Abomey-Calavi University (UAC), south Benin. Seeds were collected from three study sites (Boukoumbé in the Sudanian zone, Savalou in the Sudano-guinean zone and Sèhouè in the Guinean zone) and were grown in small plastic bags following a random block design with three replicates.

Experiment 3: *the impact of pruning on leaf morphology*. In order to assess it, ten partially pruned trees were selected in Porga (north Benin).

Environmental data

Climatic data were acquired from the Worldclim data (Hijmans et al. 2004). The 19 selected bioclimatic variables are derived from the monthly temperature and rainfall values (1950–2000 time period) in order to generate more biologically meaningful variables as these are often used in ecological niche modeling. The soil variables were extracted from top soil

Table 1 Descriptions of the eight study sites of *Adansonia digitata*

Agro-climatic zone	Study sites	Latitude	Longitude	Average rainfall (mm/year)	Annual mean temperature (°C)
Sudanian	Karimama	N12.0477°	E 3.2012°	682	28.7
	Sanpeto	N11.6185°	E 2.4415°	884	27.7
	Porga	N10.8405°	E 1.1120°	946	28.4
	Boukoumbé	N10.2295°	E 1.2275°	1,144	26.6
Sudano-Guinean	Bassila	N8.7440°	E 1.2275°	1,188	26.6
	Dassa	N7.7354°	E 2.1910°	1,166	27.4
Guinean	Sèhouè	N6.9940°	E 2.2325°	1,076	27.5
	Comé	N6.4100°	E 1.8625°	992	27.4

Climatic data were obtained from the Worldclim data (Hijmans et al. 2004). Agro-climatic zones following White (1983)

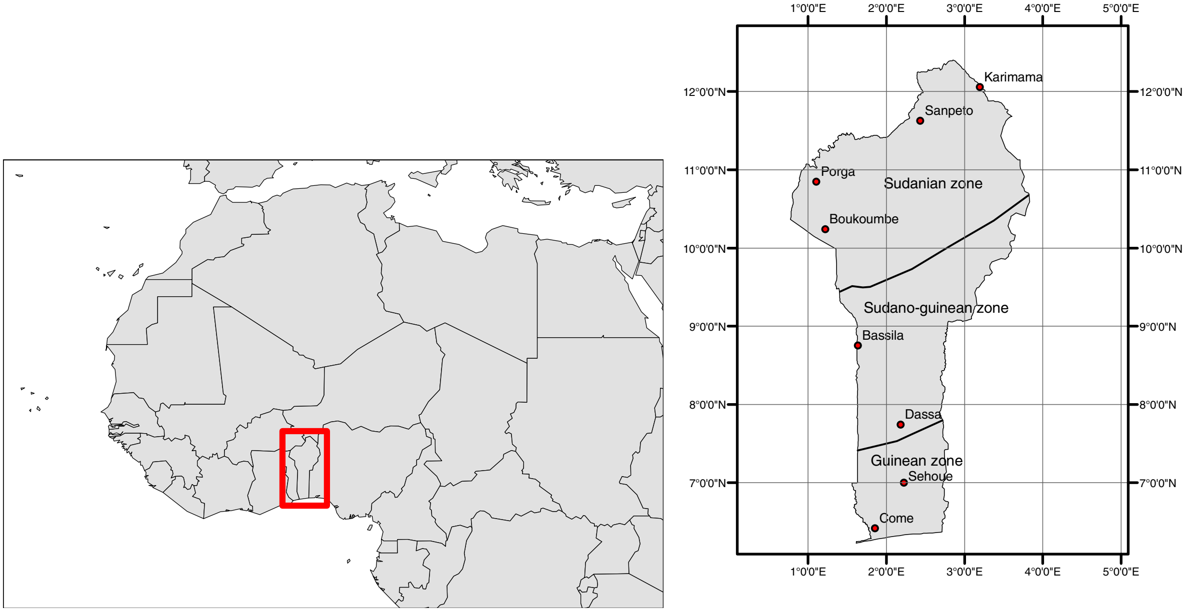

Fig. 1 Study sites of *Adansonia digitata* with respect to the agro-climatic zones of White (1983)

texture values of ISRIC derived soil parameter data set (Batjes 2002).

Morphological assessment

The morphological assessment was carried out following the same methodology in all three experiments. In experiment 1, ten fully developed leaves were selected from each tree at the lowest crown height possible, while five leaves were selected for experiment 2. In experiment 3, ten fully developed leaves were selected from pruned branches and ten leaves from non-pruned branches.

The height of each tree and the diameter at breast height (DBH) were recorded using an electronic clinometer and a decametre. Several characteristics were recorded from each leaf using a ruler and an electronic Vernier calliper: pedicel length, number of leaflets, medial leaflet length, medial leaflet length to broadest part, medial leaflet width and medial leaflet thickness measured at the widest part. The medial leaflet was punched five times with a paper punch; the discs were dried in an oven at 70 degrees and weighted with a precision balance after 48 h. The Specific Leaf Weight (SLW) was derived by dividing the dry weight of the five punched discs by their area. In order to estimate leaf shape, the ratios between medial leaflet length and medial leaflet length to broadest part (ratio 1) and the ratio between medial leaflet length and medial leaflet width (ratio 2) were calculated.

Stomata assessment

The medial leaflet was removed from three of the youngest fully opened leaves of each tree.

Nail polish impressions on the abaxial surface of the leaflets were made for all leaflet samples. Nail polish impressions on of the adaxial surface were made in order to determine whether stomata were only present on the lower surface of the leaf. The impressions were observed under a light microscope (Olympus model CHA213) and counts were made of stomata in three random fields of view, at $(10 \times 40)\times$ magnification. Ten random measurements of guard cell length were made from one leaf per tree using an eye piece micrometer at magnification $(10 \times 100)\times$.

Statistical analyses

SPSS for Windows v 16.0, ANOVA and MANOVA were used to determine significant differences between study sites. Post-hoc pair wise multiple comparisons were performed using Tukey's-*b* test and Games–Howell test. Correlations were tested using Spearman Rank Order Coefficient.

Results

Tree morphology

There were significant differences ($P < 0.01$) in tree height, DBH and in the ratio of height/DBH between study sites in experiment 1 (Table 2). In general, trees from southern study sites were taller than those from northern study sites. Trees from Comé and Sèhouè were taller than those from Karimama even though they had similar DBH. Karimama had the lowest ratio height/DBH while Bassila had the highest. Trees from Bassila were the smallest overall (the shortest and the thinnest which affected the ratio height/DBH).

There were no significant differences ($P > 0.05$) in tree height and/or basal diameter between north and south in experiment 2.

Leaf morphology

There were significant differences between study sites in all leaf morphological characteristics measured in experiment 1 (Table 3). In general, leaves from Comé, Sèhouè and Karimama were larger than those from other study sites (greater medial leaflet length, longer pedicel, more number of leaflets, thicker, higher SLW) while leaves from Porga and Dassa were the smallest. Although leaves from Boukoumbé were not the biggest, they had the highest SLW. Medial leaflet length to broadest part and the medial leaflet width followed the same pattern of medial leaflet length. Significant differences were observed in the leaf shape ratios, ratio1 and ratio 2 (results not included in Table 3). Leaves from Dassa had significantly smaller leaf shape ratios. The fact that a high percentage of leaves collected in Dassa had 3 leaflets might influence the leaf shape ratios.

Significant differences were observed in leaf size in experiment 2 (Table 4). Leaves from Savalou (central Benin) were significantly smaller than those from other sites-shorter pedicel, less number of leaflets, shorter medial leaflet length. Medial leaflet length to broadest part and medial leaflet width followed the same pattern of medial leaflet length (results not included in Table 4). In this experiment, leaves from Sèhouè (south Benin) were significantly thinner and had lower SLW. There were no significant differences ($P > 0.05$) in any of the leaf shape ratios calculated (results not included in Table 4).

In experiment 3, leaves from non-pruned branches were significantly bigger than those from pruned branches (Table 5). However, no significant differences ($P > 0.05$) were found in the leaf shape ratios. Significant differences ($P < 0.01$) were found in ML thickness and SLW, with leaves from non-pruned branches being thicker and having higher SLW.

Stomata assessment

There was a significant difference in stomata density between study sites in experiment 1 (Table 3). Bassila had the lowest stomata density while the highest

Table 2 Tree height, DBH and the ratio height/DBH of *Adansonia digitata* from eight study sites ($n = 10$)

Agro-climatic zone	Study sites	Height (m)	DBH (m)	Ratio height/DBH
Sudanian	Karimama	8.56 ± 0.77 ab	1.06 ± 0.39 b	8.14 ± 8.11 b
	Sanpeto	8.44 ± 3.62 ab	0.7 ± 0.5 ab	16.23 ± 8.11 ab
	Porga	11.46 ± 2.72 ab	0.63 ± 0.2 ab	19.60 ± 7.77 ab
	Boukombé	9.97 ± 2.42 ab	0.46 ± 0.12 ab	21.83 ± 4.29 ab
Sudano-Guinean	Bassila	5.51 ± 2.36 a	0.23 ± 0.14 a	25.92 ± 5.91 a
	Dassa	13.2 ± 4.06 b	0.76 ± 0.25 ab	17.27 ± 1.49 ab
Guinean	Sèhouè	15.07 ± 5.21 b	1.03 ± 0.35 b	16.39 ± 6.92 ab
	Comé	14.49 ± 7.14 b	0.87 ± 0.47 b	17.39 ± 2.76 ab

Means followed by the same letter within a column are not significantly different at $P < 0.01$ (Tukey's-*b* test)

DBH diameter at breast height

Table 3 Leaf morphological and stomatal characteristics of *Adansonia digitata* from eight study sites ($n = 100$)

Agro-climatic zone	Study sites	ML length (cm)	Pedicel length (cm)	No. leaflets	ML thickness (mm)	SLW (mg/cm²)	No. stomata per mm²	Guard cell length (μm)
Sudanian	Karimama	8.54 ± 1.62 a	8.10 ± 2.50 a	5.62 ± 0.90 b	0.28 ± 0.04 a	8.14 ± 1.85 a	128.26 ± 18.39 c	–
	Sanpeto	7.42 ± 1.45 c	6.12 ± 1.89 b	4.12 ± 0.97 c	0.22 ± 0.03 c	5.89 ± 1.41 c	124.08 ± 24.95 bc	–
	Porga	6.26 ± 1.26 b	4.56 ± 1.42 c	3.71 ± 0.89 d	0.24 ± 0.04 b	7.89 ± 1.58 a	146.08 ± 29.71 f	38.26 ± 4.67 b
	Boukombé	7.11 ± 1.64 c	5.68 ± 1.93 b	4.67 ± 0.84 a	0.29 ± 0.04 a	9.81 ± 1.22 d	101.09 ± 16.46 e	37.55 ± 4.03 b
Sudano-Guinean	Bassila	8.19 ± 1.90 a	6.09 ± 2.46 b	4.60 ± 0.88 a	0.25 ± 0.03 b	5.81 ± 1.43 c	75.45 ± 16.29 d	38.72 ± 4.87 b
	Dassa	6.07 ± 1.44 b	5.93 ± 2.16 b	4.28 ± 1.02 c	0.26 ± 0.04 b	6.79 ± 1.67 b	119.21 ± 17.16 bc	37.16 ± 4.32 b
Guinean	Sèhouè	8.71 ± 1.63 a	7.28 ± 1.84 a	5.39 ± 1.10 b	0.28 ± 0.04 a	8.03 ± 2.10 a	114.85 ± 17.60 b	41.97 ± 5.12 a
	Comé	8.88 ± 1.29 a	7.53 ± 2.35 a	4.74 ± 1.26 a	0.28 ± 0.05 a	8.26 ± 2.20 a	90.26 ± 16.52 a	41.22 ± 3.94 a

Means followed by the same letter within a column are not significantly different at $P < 0.01$ (Games-Howell test)

ML medial leaflet, *SLW* specific leaf weight

Table 4 Leaf morphological and stomatal characteristics of *Adansonia digitata* from three seed collection sites grown in the farm ($n = 90$, stomata No. and guard cell length $n = 30$)

	Seed collection sites	ML length (cm)	Pedicel length (cm)	No. leaflets	ML thickness (mm)	SLW (mg/cm²)	No. stomata per mm²	Guard cell length (μm)
North	Boukoumbé	11.16 ± 2.75 b	11.28 ± 3.76 c	5.51 ± 0.81 b	0.24 ± 0.03 a	6.61 ± 1.6 b	176.75 ± 17.38 a	35.84 ± 3.34 a
Center	Savalou	9.5 ± 2.29 a	7.15 ± 2.38 a	4.64 ± 0.74 a	0.23 ± 0.02 a	7.45 ± 1.74 a	172.32 ± 16.19 b	37.4 ± 3.12 b
South	Sèhouè	10.70 ± 2.6 b	9.73 ± 3.12 b	5.6 ± 0.83 b	0.21 ± 0.03 b	5.18 ± 1.39 c	144.84 ± 13.1 c	38.53 ± 3.7 b

Means followed by the same letter within a column are not significantly different at $P < 0.01$ (Tukey's-*b* test)

ML medial leaflet, *SLW* specific leaf weight

Table 5 Leaf morphological and stomatal characteristics of *Adansonia digitata* from Porga (n = 100, stomata No. n = 90)

	ML length (cm)	Pedicel length (cm)	No. leaflets	ML thickness (mm)	SLW (mg/cm^2)	No. stomata per mm^2	Guard cell length (μm)
Non-pruned branch	5.71 ± 1.2 a	4.00 ± 1.61 a	4 a	0.24 ± 0.04 a	7.79 ± 1.85 a	146.08 ± 27.98 a	38.70 ± 5.08 a
Pruned branch	10.03 ± 1.55 b	9.68 ± 2.34 b	5 b	0.32 ± 0.04 b	11.65 ± 2.40 b	165.7 ± 23.89 a	38.98 ± 5.07 a

Means followed by the same letter within a column are not significantly different at $P < 0.01$ (Tukey's-*b* test)

ML medial leaflet, *SLW* specific leaf weight

Table 6 Coefficients of correlation between stomatal characteristics and environmental variables

Environmental variables	Stomata density	Guard cell length
Annual mean temperature	0.604**	−0.012
Mean diurnal range	0.652**	−0.183**
Isothermality	0.45**	0.046
Temperature seasonality	−0.384**	−0.01
Max temperature of warmest month	−0.006	−0.189**
Min temperature of coldest month	−0.535**	0.238**
Temperature annual range	0.286*	−0.207
Mean temperature of wettest quarter	−0.066	−0.239**
Mean temperature of driest quarter	−0.402**	0.254**
Mean temperature of warmest quarter	−0.335**	0.227**
Mean temperature of coldest quarter	0.161**	−0.069
Annual precipitation	−0.442**	−0.292**
Precipitation of wettest month	−0.293**	0.158**
Precipitation of driest month	0.401	−0.254**
Precipitation seasonality	0.507**	−0.248**
Precipitation of wettest quarter	−0.16**	0.297**
Precipitation of driest quarter	0.402**	−0.254**
Precipitation of warmest quarter	0.169**	0.284**
Precipitation of coldest quarter	0.076*	0.205**
pH_{water}	−0.25**	−0.055
pH_{KCl}	−0.165**	0.02
C/N	0.238**	0.135**
% Gravel	0.176**	−0.219**
% Sand	0.562**	−0.202**
% Silt	−0.594**	0.182**

* P value < 0.05, ** P value < 0.01

stomata densities were found in northern study sites. Significantly larger guard cells were found in the southern study sites (Comé and Sèhouè). Stomata were observed next to the main nerve of the medial leaflet on the adaxial impressions in some of the samples both in southern and northern study sites although no stomata were found on the medial leaflet adaxial lamina surface.

For the second experiment, stomata density was significantly higher and guard cells were significantly smaller in the north (Table 4). A few stomata were found close to the nerves of the medial leaflet on the adaxial impressions.

For the third experiment, no significant differences ($P > 0.05$) were found in stomatal density or guard cell length (Table 5). No stomata were observed on the adaxial impressions.

Correlations

Stomatal characteristics were significantly correlated with most environmental variables selected (Table 6). Stomata density was highly positively correlated ($r_s > 0.6$, $P < 0.01$) with annual mean temperature and mean diurnal range while guard cell length was more correlated with precipitation characteristics ($r_s > 0.25$, $P < 0.01$) than temperature. Sand percentage and silt percentage were highly positively correlated ($r_s > 0.5$, $P < 0.01$) with stomata density.

Discussion

It is apparent from this study that pruning plays a role in determining the size of baobab tree leaves, as leaves from pruned branches were found significantly smaller and thinner than leaves from not pruned branches in the same trees grown in the same environmental conditions (experiment 3). However, pruning does not affect stomata density or guard cell length (see Table 5).

The differences in stomata characteristics in the *in situ* experiment are consistent with climatic differences between the study sites. Comé, situated in the Guinean zone and Bassila (situated in a humid area even though it is in the Sudanian zone, Sokpon and Biaou 2002) had the lowest stomata densities while the highest stomata densities were found in northern study sites. Abrams et al. (1990) concluded that xerophytes often have a higher stomata density than mesophytes.

Larger guard cells were found in the southern study sites where the climate is much more humid. It should be noted that baobabs from Bassila, in spite of having small guard cells, had low stomata density. Stomata density has been reported to be much more plastic than guard cell sizes, thus, Bassila trees found in a much wetter area than other northern sites adapt themselves by reducing their stomata density.

The relationship found between stomata density and climatic characteristics is in accordance with the literature: the higher the temperature, the higher the stomata density, the lower the precipitation, the higher the stomatal density. The correlation between sand percentage and silt percentage in the soil and stomata density also agrees with the literature: sandy soils hold much less water than loam and clay soils, baobab trees growing in sandy soils experienced much more drought stress than others, thus stomata density was higher.

Although correlations found between stomatal characteristics and the environmental factors indicate environmental influence on stomata characteristics, the results in this study show a certain degree of heritability of stomata characteristics. In experiment 2, even though the trees had been planted in a wetter environment (the Guinean zone), trees from the north had higher stomata density and smaller guard cell length than those from southern study sites. Teklehaimanot et al. (1998) also found a similar trend for 4 month seedlings of *Parkia biglobosa* (Jacq.) G. Don.

Even though differences in stomata characteristics could be explained by the difference in climatic conditions from north to south in the farm experiment, that was not the case for the variation in leaf size. Leaves from Savalou (the Sudano-Guinean zone) were smaller and had higher SLW than those from Boukoumbé (the Sudanian zone) although leaves from Boukoumbé were smaller and had higher SLW than those from Sèhouè (the Guinean zone). As the trees were grown in the Guinean zone, water availability was probably less of a limiting factor for survival, and trees could have bigger leaves.

In the *in situ* experiment, there was a trend, with trees from the north having smaller leaves than those from the south. Foliage age due to pruning might account for the variation in leaf size, thickness and SLW. In Karimama, Comé and Sèhouè trees were not as pruned as in other sites. In the south (Comé and Sèhouè), locals do not use daily baobab leaves for food as they do in the north (Dansi et al. 2008). Trees are not pruned in Karimama, where baobab density is high and baobab fruits are highly economically valued and exported to Niger (Assogbadjo et al. 2005a, b). Leaves from Karimama, Comé and Sèhouè apart from being bigger, were found to be always hairy, another characteristic of old foliage. Old leaves have more secondary compounds and tend to be thicker. However, leaves from Boukoumbé—in spite of being small and from pruned trees were reported to have the highest SLW, which can be related to drought tolerance. Thus, it seems that pruning and environment affect baobab leaf morphology.

Pruning might also account for the variation in tree height and diameter. Baobab trees from Bassila—very pruned were thinner and shorter than the trees sampled elsewhere. However, tree age might also explain differences in tree size. Breitenbach (1985) suggested several growth stages with different tree shape and growth rates. The high ratio height/DBH from Bassila indicates that trees from this site were much younger than trees from other sites. Although pruning and tree age might be playing a role, environment also seems to determine tree size. Trees from Karimama were significantly shorter than those from Sèhouè (in both sites trees were not pruned and had a similar diameter). Karimama, the furthest north site, is much drier than Sèhouè in the Guinean zone. In general, plants from drier environments tend to be shorter or smaller overall, compared with those of wetter environments (Abrams et al. 1990). Trees from the north planted in the farm were not significantly smaller than those from the south. In the farm, where water availability was probably less of a limiting factor to survival than competition for light, trees (from north and south) could grow taller. Light has been suggested to be a limiting factor in other baobab species growth (Metcalfe et al. 2007).

Conclusions

Results indicate that both the environment and genetics play a role on baobab drought tolerance.

When seeds from the north are grown in the south, their leaves are bigger, but their stomata characteristics do not change. Differences in stomatal characteristics seem to support a degree of physical isolation and genetic structuring of the populations of different climatic zones in Benin as suggested by Assogbadjo et al. (2006). With the aim of facilitating tree improvement, further study on baobab drought tolerance mechanisms is recommended. As current evidence suggests a variation in the degree of baobab drought tolerance, locally desirable types could be selected and incorporated into new areas.

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