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Comparison of Leaf Traits and Branching Patterns between *Acacia tortilis* (Forsk.) Hayne *subsp. raddiana* (Savi) Brenan, *Balanites aegyptiaca* (L.) Del. and *Ziziphus mauritiana* Lam. Seedlings Originated from the Sahel

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Authors' contributions

This work was carried out in collaboration between all authors. Author LÉA designed the study, and wrote the protocol. Authors FTN and AKB conducted the measurements. Author FTN wrote the first draft of the manuscript. Authors VG and FTN managed the literature searches. Author VG performed the statistical analyses and discussed the conclusion. All authors read and approved the final manuscript.

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ABSTRACT

Aims: The aim of this study was to compare the leaf traits and branching patterns between *Acacia tortilis*, *Balanites aegyptiaca* and *Ziziphus mauritiana* seedlings, three species occurring in the same range in the Sahel, a semi-arid tropical area of Africa.

Study Design: Seeds used in this experiment were collected from a semi-arid area (16°20'N, 15°25'W), from species growing in their natural range in the Sahel. Seeds were after transferred at the experimental site where they were germinated and grown in a common garden experiment, on an area of 1300 m².

Place and Duration of Study: The experimental site was located at around 400 km south of the seed origin (17°33'N, 14°55'W). The experiments were carried out between October 2002 and October 2004.

Methodology: The seedlings were watered three days a week from the beginning of the experiment until July 2004. Thereafter, seedlings were assessed at 11 months, 16 months old, and at 24 months after the seed germination date. In the assessment, we measured the length (L_{GU}) and the number (N_{GU}) of growth units, the number of nodes (N_{node}), and leaves (N_{leaf}), and the single (A_{leaf}) and total ($A_{foliage}$) leaf areas.

Results: Following the water stress, N_{leaf} and A_{leaf} only decreased in *A. tortilis*, to tightly control the transpiration. A_{leaf} increased in *B. aegyptiaca* and *Z. mauritiana*, due to persistent leaves flushed before the water stress. $A_{foliage}$, N_{GU} and N_{node} were generally consistent, while L_{GU} decreased in *B. aegyptiaca*. The defoliation in dry season despite the watering suggested an endogen control, allowing the species to escape harsh conditions in their natural range.

Conclusion: The study do not support the hypothesis according to which species naturally coexisting are likely to display similar trend in leaf traits and branching patterns in response to drought. The study has been limited to three weeks of water stress and deserves to be extending to provide more insight into traits pattern for a longer period of water stress.

Keywords: Drought; growth units; leaf area; phenology; tropical area.

1. INTRODUCTION

The Sahel is one of the driest savanna ecozones with high inter-annual rainfall variability, ranging from 200 to 400 mm, high potential evaporation of about 2000 mm year^{-1} and a deep groundwater of more than 30 m [1]. The rainy season spans from July to September, and the dry season from October to June. The mean annual maximum temperature is between 35-37°C with a peak up to 48°C, and the minimum between 13-15°C [2]. Rainfall is one of the main limiting factors, explaining the highly variable recruitment potential generally occurring in semi-arid savannas [3]. Leaf traits are associated with resistance to drought [4] and can be used to assess species vulnerability to water shortage.

Acacia tortilis (Forsk.) Hayne, *Balanites aegyptiaca* (L.) Del., and *Ziziphus mauritiana* Lam. are multipurpose tree species naturally occurring in the Sahel, with leaf traits adapted to frequent water stress. They are used by the local population as fodder for livestock, as food and herbal medicine. The genus *Acacia* is particularly known to produce commercial gum, generating substantial income for local population [5]. In search for the sustainability for these species in the context of advance aridification due to climate change, there is a growing interest to better know the functional and morphological traits allowing these species to cope with drought regularly occurring in these areas. Their phenology is closely linked with climate including drought and can be used to provide insight into species response to drought.

Several studies on mature Sahelian native species [6-8] focused on qualitative phenology based on visual assessment of leafing patterns in relation with climate. Hence, *A. tortilis* is a semi-evergreen [7,9], whereas *B. aegyptiaca* (L.) Del. is an evergreen species [9,10]. *Z. mauritiana* Lam. is sometimes considered as semi-evergreen [8,9], or deciduous [11]. Leaves generally flush at the end of the dry season, when the water availability at the soil surface is completely depleted for *A. tortilis* [7,9], *B. aegyptiaca* [8] and *Z. mauritiana* [8,9]. While *A. tortilis* [7] and *Z. mauritiana* [8,12] have their maximum leafing in the earlier rainy season and lasts until the middle of the dry season, *B. aegyptiaca* remains green all year round [8].

Water stress reduces the duration of full canopy stage for *A. tortilis* [7], while we did not find such evidence in *B. aegyptiaca* and *Z. mauritiana*. These patterns were described in mature trees and may not necessarily be translated into seedlings because the direction of the responses may be changing according to the species ontogeny. Water stress significantly reduces leaf area in *A. tortilis* seedlings [13], leaf area and leaf weight in *B. aegyptiaca* [14], and leaf area in *Ziziphus* sp*.* [15], suggesting that stress conditioning enhances adaptive traits for drought tolerance [14]. However, there are still uncertainties about the comparative traits patterns in response to drought among *Acacia tortilis*, *B. aegyptiaca* and *Z. mauritiana*. Species naturally coexisting in the same area are believed to display similar strategies to cope with water stress, which allow them to adapt to similar habitats and form the niche differentiation [16]. In this study we aimed to know the extent to which *Acacia tortilis*, *B. aegyptiaca* and *Z. mauritiana* differ in response to same stress.

2. MATERIALS AND METHODS

2.1 Study Site, Seeds Collection and Climate

2.1.1 Site description

A. tortilis, *B. aegyptiaca* and *Z. mauritiana* naturally occur in the Sahel ecozone of Senegal. Their seeds were collected near Souilène village (16°20'N, 15°25'W) located 20 km south of Dagana where there is a weather station that is used as reference for the zone (Fig. 1). The dry season spans from October to June, and the rainy season from July to September. Annual rainfall averages 280 mm. The dry season can be subdivided into a hot dry season in May with average maximum and minimum temperatures of 41 and 22.8°C respectively, and a cool dry season in January with respective maximum and minimum temperatures of 31 and 14.8°C (annual average = 28.8°C). The soils are sandy with a deep water table [7].

2.1.2 Seeds collection

The collected seeds were germinated and their seedlings transferred in the experimental site located in the Institut de Recherche pour le Développement (IRD) of Bel-Air in Dakar 17°33'N, 14°55'W, at about 400 km south of the seed origin (Fig. 1).

Soils of the experimental site are tropical ferruginous, non-washed [17], slightly basic (pH = 8.35) resting on sandy sedimentary substratum, and contain 0.92% of organic matter, 0.53% of organic carbon and 0.46% of nitrogen [18]. The cold Canary current and the maritime trade winds moderate the climate [1]. Total annual rainfall is 376.3 mm, lowest temperatures are noted in January-February (20.7°C), and highest in September-October (27.7°C).

2.1.3 Climate

In 2002, 2003, and 2004, monthly mean maximum temperatures were around 28°C and usually occurred in rainy season while monthly mean minimum temperatures (21°C) were noted in the dry season around January and February (Fig. 3). Also, monthly mean vapor pressure displayed a minimum in the dry season (18×10^{-1}hPa) and a peak in the rainy season (30×10^{-1}hPa). In 2002, total annual rainfall was 151 mm but the seedlings were transplanted in the late rainy season, exactly the first week of October when was recorded only 4 mm of rain before the end of the rainy season. In 2003 the rainy season spanned from June to October with total amount of rainfall of 385 mm. In 2004, 234 mm of rainfall were recorded between June and October when dropped a last significant rain of 4 mm. The seedlings consecutively remained almost 3 weeks without additional water.

2.2 Experimental Design and Measurements

In order to obtain a uniform and high germination rate, pretreatments were performed on seeds before sowing for germination. The seeds of *A. tortilis* were pre-treated with sulphuric acid for 60 minutes and soaking in cold water for 10 to 15 minutes. Seeds of *B. aegyptiaca* and *Z. mauritiana* seeds were pre-treated by removing the impermeable seed coats and soaking in cold water for 24 hours. In August 2002, the pretreated seeds were germinated in plastic bags filled with sand and soil mixture, at a rate of one seedling per plastic bag in a nursery located in the Centre National de Recherches Forestières (CNRF / ISRA, Dakar). The germination was followed by a nursery acclimation phase (September 2002, end of rainy season), and two months from the germination date the seedlings were transplanted in the experimental site of IRD.

The experiment was carried out in an open area of 1300 m² (65 m × 20 m). To account for mortality in the course of the experiment, we planted more seedlings than we really need for the experiment (Fig. 2). All seedlings were planted at a spacing of 2 m by 1.3 m to reduce competition during the experiment [19,20]. In total, 96 seedlings of *A. tortilis*, 72 seedlings of *B. aegyptiaca*, and 84 seedlings of *Z. mauritiana* were planted in the experimental site (Fig. 2).

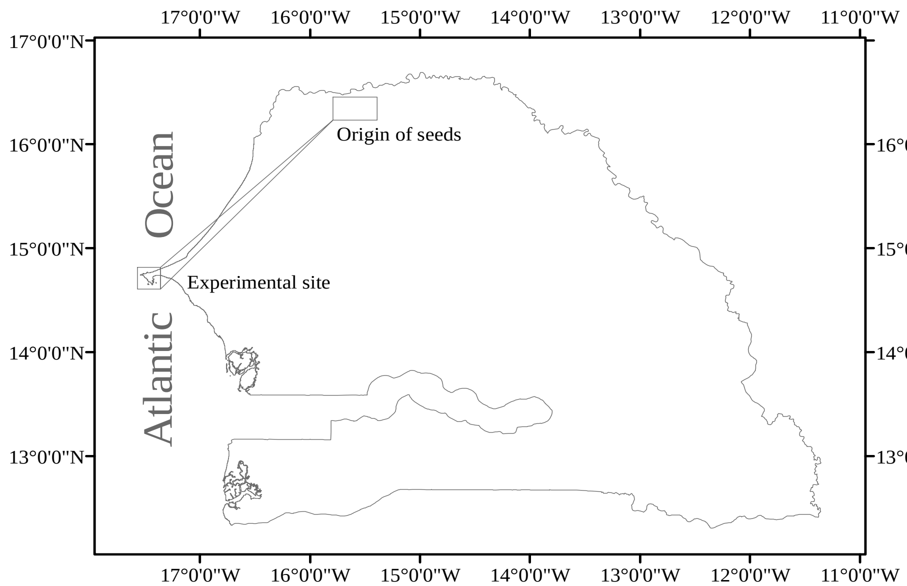

Fig. 1. Origin of the seeds of *A. tortilis, B. aegyptiaca* and *Z. mauritiana* from their natural stands, and location of experimental site approximately (Dakar, Senegal), 400 km south of the seeds origin

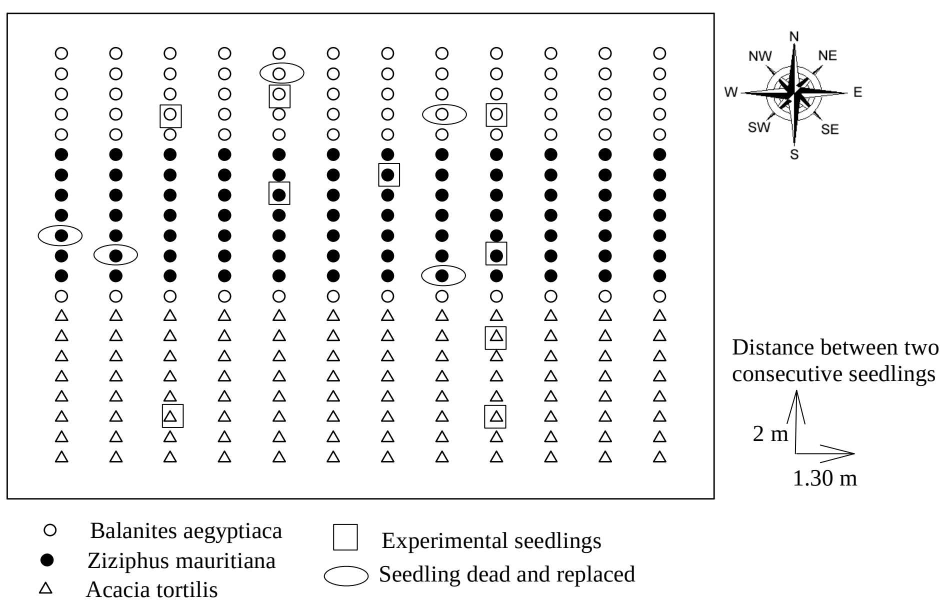

Fig. 2. Experimental design in an open area located in the Institut de Recherche pour le Développement (IRD) of Bel-Air, Dakar 17°33'N, 14°5 5'W. Two month old seedlings of *A. tortilis, B. aegyptiaca* and *Z. mauritiana* were directly transplanted in the soil, after germination and acclimation in a nursery

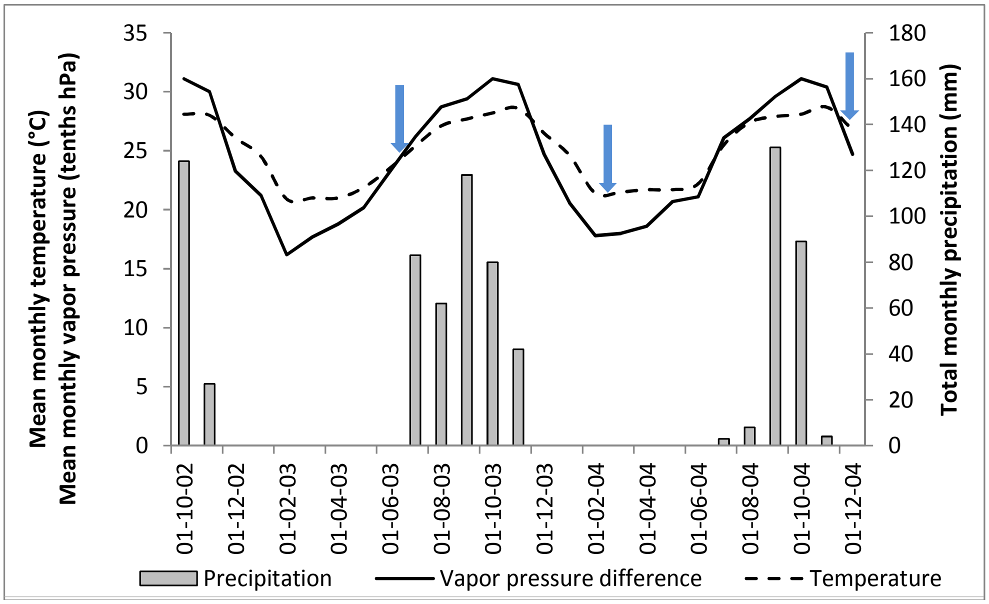

Fig. 3. Total monthly rainfall, average monthly temperature and vapor pressure of the experimental site (17°33'N, 14°55'W). The reference weather station is located in Dakar-Yoff, at 12 km far as a crow flies from the experimental site. Data came from the monthly climatic data for the World 2002−04 (WMO-NOAA, 2002−04). The arrows indicate the measurement dates

In order to build models to estimate leaf areas, leafy twigs were destructively sampled randomly in three individuals different from the measured seedlings. The sampled twigs were stored in small refrigerated containers until they were brought to the laboratory where the projected leaf areas were measured using a leaf area meter (Model AM1, Delta-T Devices, Cambridge, UK). Linear regression models were consecutively performed then used to estimate the areas of the leaves followed in the non-destructive measurements.

On 3 month old seedlings, non-destructive measurements were carried out from October 2002 to October 2004, on 3 seedlings per species selected randomly. In tree architecture model, when an episode of continuous twig elongation is followed by an interruption of growth, it produces a morphological marker of growth interruption. A Growth Unit (GU) is the section of twig delimited by two consecutive morphological markers of growth interruption [21]. A growth unit is constituted of a succession of nodes and internodes and is defined by its order in the branching ramification pattern. Hence, along a given leafy axis, we defined a GU of order 1 as the one closer to the main stem. It bears a GU of order 2, followed by a GU of order 3 and so one, until the tip of the leafy axis. In the followed seedlings, all the different orders of growth units (GU) were numbered and marked from the top of the branches and progress downwards until the main stem. The seedlings were watered three days a week from the beginning of the experiment until July 2004 (beginning of rainy season) when the watering was withheld, making the rains the only source of water provision, until the end of the experiment at 26 months from the germination date. The seedlings were measured at three different dates. The first measurement was carried out in 11 month old seedlings (M_{11}), the second measurement in 16 month old (M_{18}), and the third one in 26 month old seedlings (M_{26}) (Fig 3).

In every measurement date, we counted the number of nodes and leaves of the GU. Since *B. aegyptiaca* has simple leaves and *Z. mauritiana* is made up only of two leaflets, the leaf length and the maximum width perpendicularly to the central rib were measured. *A. tortilis* has compound leaves so that number of leaflets was also counted. Single leaf area was estimated using the regression models obtained by the destructive sampling, to derive an average value for the GU. Total number of leaves and leaf area of a given seedling were obtained by adding the values of all the GU of the seedling. Total length of GU was obtained by summing up all the GU of the seedling.

2.3 Statistical Analyses

A two-way analysis of variance was performed using the GLM procedure of the SAS software package version 9.3, according to the model:

$$Y_{ijk} = \beta_0 + \beta_1 S_i + \beta_2 GU_{ij} + \beta_3 M_{ijk} + \beta_4 SM_{ijk} + \varepsilon_{ijk}$$

Where Y is the dependent variable and represents the total number of leaves, average single leaf area, total leaf area, total number of GU, total GU length, and total number of nodes per seedling. The subscripts i, j, and k represent the species, GU rank, and month respectively. The fixed effects of the model are represented by S, GU, and M respectively for the species, GU, and month. β_0 is the intercept, β_1 to β_4 the estimates for the fixed effects, and ε_{ijk} is the error term ($\varepsilon_{ijk} \sim N(0;\sigma^2)$). Interaction between S, M and GU was not considered due to low replicate of GU ending with insufficient degree of freedom. An effect was considered significant at P<0.05 based on a type III F-test on the fixed effects. When a fixed effect was significant, paired-comparisons between species, and month were performed with a t-test (P<0.05) using the LSMEANS statement and PDIFF option of SAS software.

3. RESULTS

3.1 Leaf Area Estimation Models

The linear regression models predict well the single leaf area for *A. tortilis*, *B. aegyptiaca* and *Z. mauritiana* (Table 1).

3.2 Total Number of Leaves per Seedling

The species (F = 30.32, P<0.001) and the month (F = 5.06, P = 0.014) had significant effects on the total number of leaves (N_{leaf}) while the interaction species × month was not significant (Table 2).

For *A. tortilis*, N_{leaf} were 96, 66 and 63 in M_{11}, M_{18} and M_{26}, respectively (Fig. 4). Significantly lower N_{leaf} were noted in M_{18} (P = 0.05) and M_{26} (P = 0.03) relatively to M_{11}, while no difference was noted between M_{18} and M_{26}. For *B. aegyptiaca* and *Z. mauritiana* N_{leaf} hardly varied for the duration of the experiment. *A. tortilis* had all the time significantly higher N_{leaf} than *B. aegyptiaca* (P<0.001) and *Z. mauritiana* (P<0.001). The water stress reduced N_{leaf} by 5% in *A. tortilis* and 83% in *B. aegyptiaca*, whereas an increase of 62% was noted in *Z. mauritiana*.

3.3 Average Single Leaf Area

The species, the month and the interaction between species and month had significant effects on the average single leaf area (A_{leaf}) as shown in Table 2. *A. tortilis* displayed a quite constant A_{leaf} of about 0.31 cm^2 in average over the three measurement dates (Fig. 4). For *B. aegyptiaca*, A_{leaf} were 0.56, 1.38 and 1.72 for M_{11_wet}, M_{18_wet} and M_{26}, respectively. Relatively to M_{11_wet}, significant increase of A_{leaf} was noted in M_{26}, (P = 0.008), but no difference was observed between M_{18_wet} and M_{26}. For *Z. mauritiana*, A_{leaf} were 0.30, 0.33 and 2.29 for M_{11}, M_{18} and M_{26}, respectively. In M_2, A_{leaf} significant increased relatively to both M_{11} (P<0.001) and M_{18} (P<0.001). The three species showed similar A_{leaf} in M_{11}. In M_{18}, only *A. tortilis* displayed significantly lower A_{leaf} than *B. aegyptiaca* (P = 0.031).

3.4 Total Leaf Area of Seedlings

Only the month had a significant effect (Table 2) on the total seedling leaf area ($A_{foliage}$). The average $A_{foliage}$ were respectively 26.92 and 28.24 cm^2 in *A. tortilis* and *B. aegyptiaca*, with no significant fluctuations over the three measurement dates (Fig. 4). For *Z. mauritiana*, $A_{foliage}$ were 9.05, 2.21 and 74.57, in M_{11}, M_{18} and M_{26}, respectively. A significant increase was noted in M_{26} relatively to M_{11} (P = 0.013). Overall, $A_{foliage}$ did not significantly vary between species.

3.5 Total Number of Growth Units per Seedling

Growth units differed significantly among species (Table 2). Total number of growth units (N_{GU}) slightly decreased in *A. tortilis* and increased in *B. aegyptiaca*, and *Z. mauritiana*, but the effects of water stress were not significant. N_{GU} had average values of 10 in *A. tortilis*, 21 in *B. aegyptiaca*, and 14 in *Z. mauritiana*. The three species showed no significant difference in M_{11}. Following the water stress, *A. tortilis* had significantly lower N_{GU} than *B. aegyptiaca* (P = 0.005) and *Z. mauritiana* (P = 0.037), while all other differences between species were insignificant.

3.6 Total Length of Growth Unit per Seedling

The species, GU, and month had significant effects (Table 2) on the total length of GU (L_{GU}). L_{GU} was in average 21.67 cm in *A. tortilis* with no significant variations (Fig. 5). For *B. aegyptiaca*, L_{GU} were 25, 79, and 47 in M_{11}, M_{18} and M_{26}, respectively. L_{GU} significantly increased from M_{11} to M_{18} ($P<0.001$), and decreased from M_{18} to M_{26} ($P = 0.024$). For *Z. mauritiana*, L_{GU} were 9, 54, and 26 for M_{11}, M_{18} and M_{26}, respectively. A significant increase was noted between M_{11}, and M_{18} ($P = 0.005$). In M_{11}, L_{GU} did not vary between the three species. However, *A. tortilis* had significantly shorter GU than *B. aegyptiaca* in both M_{18} ($P = 0.004$) and M_{26} ($P = 0.04$).

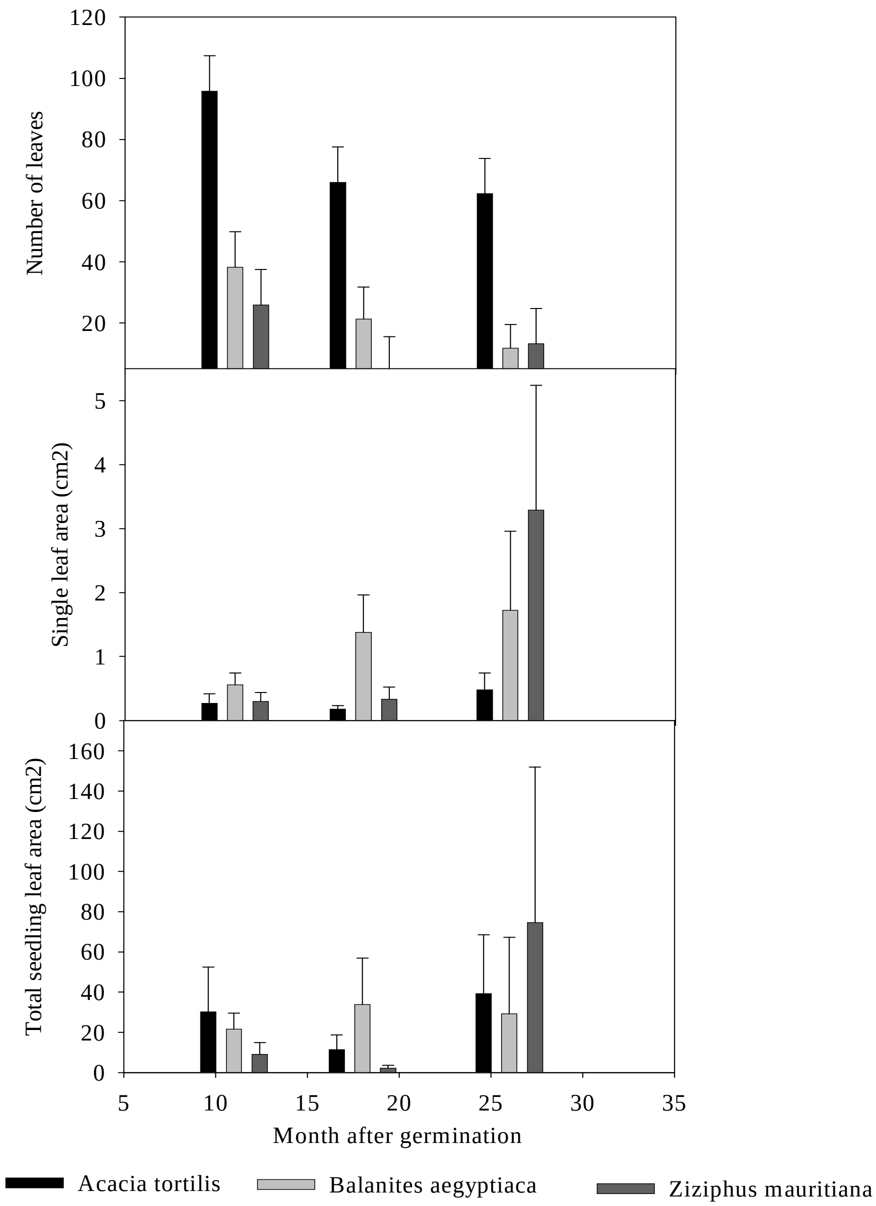

Fig. 4. Number of leaves, single leaf area, and total leaf area followed on seedlings from their germination to 26 month old in *A. tortilis, Z. mauritiana*, and *B. aegyptiaca* in a semi-controlled experiment. Seedlings were watered from the start of the experiment until month 23; when the watering was withheld at the beginning of the rainy season until month 26. Error bars represent standard errors

Table 1. Linear model of assessment of the single leaf area (A_{leaf}, cm^2) of 24 month old seedlings of *A. tortilis*, *B. aegyptiaca* and *Z. mauritiana*

Species	Prediction model of A_{leaf}	N	R^2	P
A. tortilis	$0.164 \times (L_{leafstalk}) + 0.164 \times (N_{leaflet}) – 0.523$	228	0.61	P<0.001
B. aegyptiaca	$1.040 \times (L_{leaf}) + 1.999 \times (W_{leaf}) – 4.639$	109	0.84	P<0.001
Z. mauritiana	$1.493 \times (L_{leaf}) + 3.437 \times (W_{leaf}) – 5.759$	130	0.96	P<0.001

Note: N = total number of leaves, $L_{leafstalk}$ = length of the leafstalk (cm), $N_{leaflet}$ = number of leaflets, L_{leaf} = leaf length (cm) and W_{leaf} = leaf width (cm), the R^2 were 0.61, 0.84, and 0.96 in A. tortilis, B. aegyptiaca and Z. mauritiana, respectively. These high R^2 associated with significant p-values indicated a good prediction capability of the models

Table 2. Two-way ANOVA of the effects of Species, GU rank, month and the interactions Species × Month on the leaf and growth unit traits in a semi-controlled experiment on seedlings of *A. tortilis*, *B. aegyptiaca* and *Z. mauritiana*

Source	df	Anova SS	Mean square	F value	P>F
Number of leaves per seeding					
Species	2	25610.40	12805.20	30.32	< 0.001
GU rank	6	2770.94	461.82	1.09	0.392
Month	2	4174.05	2087.02	4.94	0.015
Species × Month	4	668.57	167.14	0.40	0.810
Average single leaf area					
Species	2	9.10	4.55	6.38	0.006
GU rank	6	4.11	0.68	0.96	0.471
Month	2	18.05	9.02	12.65	< 0.001
Species × Month	4	11.69	2.92	4.10	0.011
Total leaf area per seedling					
Species	2	215.40	107.70	0.09	0.911
GU rank	6	3050.17	508.36	0.44	0.848
Month	2	8655.11	4327.55	3.72	0.038
Species × Month	4	6663.05	1665.76	1.43	0.252
Total number of growth units per seedling					
Species	2	772.76	386.38	3.87	0.0313
GU rank	6	8737.37	1456.23	14.58	< 0.001
Month	2	35.55	17.77	0.18	0.838
Species × Month	4	675.04	168.76	1.69	0.177
Total length of growth units per seedling					
Species	2	6968.01	3484.01	6.53	0.004
GU rank	6	51363.02	8560.50	16.05	< 0.001
Month	2	12193.38	6096.69	11.43	< 0.001
Species × Month	4	1176.29	294.07	0.55	0.700
Total number of nodes per seedling					
Species	2	2058.50	1029.25	12.03	<0.001
GU rank	6	14840.63	2473.44	28.92	< 0.001
Month	2	3300.21	1650.11	19.29	< 0.001
Species × Month	4	194.56	48.64	0.57	0.688

Note: GU = Growth unit

3.7 Total Number of Nodes per Seedling

Significant effects of species, GU and month were noted in the number of nodes (N_{node}). For *A. tortilis*, N_{node} were 25, 43 and 44 in M_{11}, M_{18} and M_{26}, respectively (Fig. 5), with a significant positive shift in M_{18} (P = 0.019) and M_{26} (P = 0.01) compared to M_{11}. *B. aegyptiaca* had 6, 36 and 36 nodes in M_{11}, M_{18} and M_{26}, with significant increase in M_{18} (P<0.001) and M_{26} (P<0.001) relatively to M_{11}. For *Z. mauritiana*, N_{node} were 7, 25, and 26 in M_{11}, M_{18} and M_{26}, respectively. However, relatively to M_{11}, N_{node} significantly increased in M_{18} (P<0.008) and M_{26}

(P<0.006). *A. tortilis* had significantly lower N_{node} than *B. aegyptiaca* (P = 0.05) in M18. Following the water stress, *A. tortilis* showed significantly lower N_{node} compared to *B. aegyptiaca* (P = 0.005) and *Z. mauritiana* (P = 0.037).

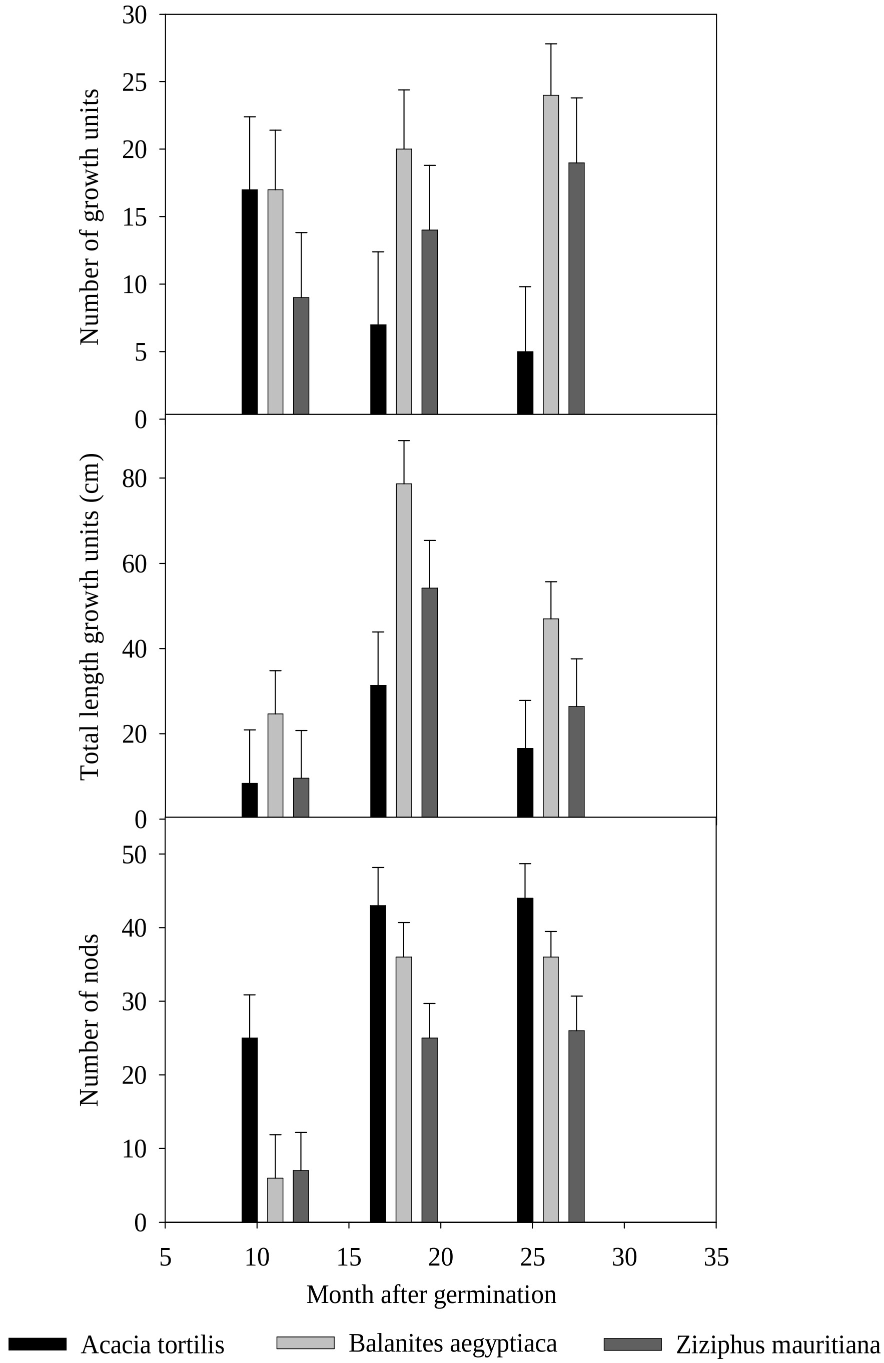

Fig. 5. Number of growth units, their total length, and the number of nodes followed on seedlings from their germination to 26 month old in *A. tortilis, Z. mauritiana*, and *B. aegyptiaca* in a semi-controlled experiment. Seedlings were watered from the start of the experiment until month 23; when the watering was withheld before the rainy season until month 26. Error bars represent standard errors

4. DISCUSSION

This study aimed to compare leaf traits and branching patterns between *A. tortilis*, *B. aegyptiaca* and *Z. mauritiana* seedlings, three species naturally occurring in the same area. Two main information can be drawn from this study. The first one pertains to the patterns displayed within one species, and the second one lays on the difference between species in their response to drought.

4.1 Variation within Species

Despite the favorable soil water status due to the watering, all the species shed their leaves, even slightly, in the dry season, but not translating into total leaf area reduction. In their natural range, a systematic defoliation also occurs in hot dry season for *A. tortilis* [7], and *Z. mauritiana* [9]. *B. aegyptiaca* also shed its leaves in hot dry season but defoliation overlaps with the next leaf flush [9]. In addition, a systematic defoliation of *A. tortilis*, grown in the Negev where it was introduced, occurs when soil water status is locally favorable, corresponding to the hot dry season of their origin in Africa [22]. The defoliation at least for *A. tortilis* may therefore be related to an endogen control, and the same mechanism may have played for *B. aegyptiaca* and *Z. mauritiana*, as well. In their natural range where drought is real at this time of the year, this could be seen as an escape strategy because maintaining lower foliage in hot dry season is conducive to some extent to tight regulation of leaf transpiration. Hence, soil water availability is seldom, if ever, to be the only variable explaining leaf shading in dry season.

B. aegyptiaca and *Z. mauritiana* increased their growth unit lengths in the middle of the dry season in response to favorable soil water availability while *A. tortilis* showed a stronger seasonality of its GU elongation. This also indicates that *B. aegyptiaca* and *Z. mauritiana* elongate their twigs in dry season to be able to respond to soil water experimentally increased in this period. Following the water stress, the GU length only decreased for *B. aegyptiaca* suggesting the active phase of GU elongation in dry season and the plastic behavior to water stress of this species. Based on GU patterns, *Z. mauritiana* displayed higher tolerance to stress as shown by its consistent GU elongation despite water stress. The greater number of GU and nodes in *A. tortilis* consecutively to water stress resulted in reduced internode distances, ending up with a greater number of nodes per unit of leafy axis. The study illustrates the statement according to which, measurement of shoot or twig is an effective way to assess fine scale plant response to environmental stimuli [23].

4.2 Variation between Species

The water stress was followed by a marked decrease in single leaf area for *A. tortilis*, but an increase for *B. aegyptiaca* and *Z. mauritiana*, however not resulting in significant variation in total leaf area. However, the slight defoliation generally observed, was enough to maintain a consistent total leaf area despite the significant change in single leaf area in the three species. *A. tortilis* had generally more leaves than *B. aegyptiaca* and *Z. mauritiana* all the time, even before the stress was applied. Earlier studies have reported leaf area decrease due to water stress in *A. tortilis* [13], *B. aegyptiaca* [24] and *Ziziphus* [15]. Water stress has been shown to reduce leaf area through reduced leaf initiation, leaf size and leaf production rate [13]. We also observed in *A. tortilis* a reduced leaf production rate, even if it was not significant. The advantage of having higher number of leaves associated with lower size single leaf areas is to allow more plasticity in leaf surface area regulation. Small leaves ensure for convective heat loss that improves cooling in hot, dry conditions, and a tight control of transpiration [25].

Unexpectedly, *Z. mauritiana* had greater single leaf areas following the water stress. *B. aegyptiaca* also positively reacted to water stress, but in comparison with first measurement date and not the second. The greater single leaf area can be explained by the fact that leaves earlier flushed when the trees were not stressed still persisted when the water stress occurred. To be able to increase their single leaf area while maintaining a consistent total leaf area following the water stress, *B. aegyptiaca* and *Z. mauritiana*, have to shed proportionally their leaves to balance their single leaf area increase. After the rainy season of 2004 with 234 mm of rainfall, the seedlings remained 3 weeks without additional water in soil. *B. aegyptiaca* and *Z. mauritiana* may have kept their leaves flushed during this previous rainy season or sooner while the seedlings were still watered. Three weeks of water stress seemed to be too short for *B. aegyptiaca* and *Z. mauritiana* to shed their leaves, showing that they can withstand water stress, longer than *A. tortilis*.

4.3 What can we Learn so Far?

A. tortilis, *B. aegyptiaca* and *Z. mauritiana* naturally occur in the same range characterized by harsh climate conditions with frequent drought episodes. They have sclerophillous leaves and can withstand severe water stress. Two clear patterns emerge from this study. *A. tortilis* bears more leaves which are also smaller than those of their counterparts, as a strategy to cope with soil water depletion. *B. aegyptiaca* and *Z. mauritiana* withstand water stress by keeping larger single leaf area, because they might have kept their greater size leaves flushed whether during the previous rainy season or earlier when the seedlings were still watered. In addition, *B. aegyptiaca* decreased its GU length following the water stress. Overall, larger plasticity in response to drought was observed in *A. tortilis* compared to *B. aegyptiaca* and *Z. mauritiana*. In addition, within a given species, the same seedlings were followed during the course of the experiment, at different ages. However it is unlikely that the age of the seedlings influenced the leaf size, since individual leaf area was shown to have a modest increase with plant size [26]. In a typical common garden experiment, many provenances are grown in a common area to study the phenotypic variability. In our experiment, the seeds which have been germinated were rather collected in a restricted area where the species naturally coexist. The differences in leaf traits and branching patterns may therefore not be attributed to a genetic variability leading to a phenotypic divergence within the species.

5. CONCLUSION

In the Sahel, a semi-arid tropical area of Africa where we collected the geminated seeds used in this experiment, soil water availability is the main environmental driving factor. *A. tortilis*, *B. aegyptiaca* and *Z. mauritiana* naturally coexist in these areas and the understanding of how they cope with water shortage is essential to implement guidelines for a more efficient assisted recruitment. This study provides to these purposes important information on leaf traits and branching patterns related to soil water availability. In contrast with what we hypothesized, species naturally coexisting do not necessarily displayed similar trend in leaf traits and branching patterns in response to drought. Although straightforward, the study was limited to three weeks of water stress. Perspectives for future studies suggest extending the drought period.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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