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DROUGHT STRESS ADAPTIVE RESPONSES OF SIX SHORT-CYCLE COWPEA VARIETIES GROWN IN TOGO

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ABSTRACT: *Drought stress is a major hindrance to cowpea cultivation. In Togo, climate fluctuations lead to sudden droughts, posing a real threat for this crop. This survey aimed to evaluate the effects of an induced water deficit in 6 short-cycle cowpea cultivars grown in Togo (Amélassiwa, Ketcheyi, Ketcheyi-Soukpelo, Malgbong-Bomoine, Siéloune, and TVX). The experimental device, under semi-controlled conditions, was a split plot (three repetitions, two treatments) with two interacting factors, varietal type and water regime. Plants in the flower initiation phase were subjected to a water deprivation of 30% of available water content (AWC) for 14 days. Plants used as control were irrigated at 70% of AWC. The fluctuations in growth parameters, total proteins, proline, malondialdehyde (MDA) levels, and yield variables were determined, and the data were analysed through ANOVA, Tukey HSD, and principal component analysis (PCA). The Fisher-Maurer index, or drought susceptibility index (DSI), was used to distinguish drought-tolerant from susceptible varieties. As a result, ANOVA revealed a significant effect ($p < 0.05$) of water deprivation on physiological and agronomic variables, except for the main root length variable. Regarding biochemical markers, a significant effect of water deficit was noted on MDA level but not on total protein and proline levels ($p > 0.05$). However, a negative correlation between both contents was noted. PCA revealed that varieties that exhibited higher yields were correlated with proline content, while those that showed higher productivity and MDA levels were correlated with protein content. Thus, osmotic adjustments mechanisms are important aspects to target first during variety improvements. According to DSIs and PCA, the six varieties can be divided into three categories: susceptible varieties (Ketcheyi and Amélassiwa), medium-tolerant varieties (Siéloune, Malgbong-Bomoine, and TVX), and high-tolerant varieties (Ketcheyi-Soukpelo).*

KEYWORDS: Cowpea, water deficit, drought stress, DSI, drought tolerance.

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INTRODUCTION

Grown in dry and semi-arid countries, including Guinea, cowpea, or *Vigna unguiculata (L.) Walp.*, is a key food crop in sub-Saharan Africa (Soule, 2002; Owade et al., 2020). It is a good source of protein, carbs, folate, vitamins, antioxidants, fibre, and other nutrients that help keep populations' diets balanced. Additionally, it can be used as animal feed fodder (Dugje et al., 2009; Sanfo et al., 2020). It enhances soil fertility and is often integrated into many processed goods made from different portions of the cowpea plants.

According to FAO statistics (FAOSTAT, 2024), global cowpea crops exceeded 9.77 million tons in 2022 from a cultivated area of about 15.19 million hectares, with a significant share of Africa accounting for 95.4% of production. In Togo, cowpea crops have increased from 45,000 tons in 2000 (Soule, 2002) to 383,664 tons in 2021 (MAEDR, 2021). Despite this increase, the national average market price of cowpea has increased, reflecting insufficient supply and production for a growing population. Besides, the yield per hectare is low. For several decades, Togo has been facing climatic fluctuations characterised by a spatial and temporal irregularity of rainfall (Badjana et al., 2014; Koudahe et al., 2017), leading to declines in agricultural yields (Mikémina, 2013; Edou, 2021).

Some studies revealed the existence of drought-susceptible genotypes. For instance, in Togo, two studies conducted first by Aziadekey et al. (2014) and later by Yorikoume et al. (2018) revealed that the yield variables of the line IT 98K-412-13 and the varieties VITOCO, VITA5, and IT87D-10-10 are significantly affected by water deficit. Currently, all promoted varieties in Togo (TVX, VITA5, VITOCO, NAFI SAM, and WANG-KAI) are improved varieties that have been introduced due to their characteristics: high productivity and earliness (Dagnon, 2018; MAEDR, 2021). However, research showed that local abiotic and biotic stressors in host ranges could reduce the yield of introduced varieties that are improved (Kamara et al., 2008). In addition, the use of imported varieties predisposes to the risk of renunciation and then disappearance of local varieties, of which Dagnon (2018) has characterised 70 genotypes. How do these locally characterised cowpea varieties respond to water deficit?

In a context of global change and climatic instabilities, it is important to identify valuable and performing varieties and set up plant resources conservation mechanisms. The purpose of this study was to assess stress responses in six short-cycle cowpea cultivars grown in Togo, understand the adaptation mechanisms of some of these local varieties, and identify tolerant and susceptible varieties, thereby contributing to breeding programs (for tolerant varieties) and an effective irrigation strategy (for susceptible varieties).

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LITERATURE REVIEW

Water deficit refers to a state where the water available is insufficient to meet plants physiological needs, leading to stress. Stress thresholds vary: 0 to –0.3 MPa, well-watered, no stress (Taiz et al., 2015); –0.3 to –0.8 MPa, mild stress, stomata begin to close (Kramer & Boyer, 1995); –0.8 to –1.5 MPa, moderate to severe (Chaves et al., 2003) and permanent wilting point (< –1.5 MPa) (Taiz et al., 2015). Fu et al. (2024) reported that the average critical soil moisture threshold (θ_{npt}), at which plants start reducing evapotranspiration, is approximately 0.19 m^3/m^3. This value corresponds to about 30–35% of volumetric soil moisture. In leaves, for a relative water content (RWC) > 90 %, plants feel no stress; 80–90%: mild stress; 70–80%: moderate stress; and RWC < 70%: severe stress—a threshold for serious physiological dysfunction (Barrs & Weatherley, 1962; Jones, 2007).

Therefore, water deficit causes a slowdown in growth and negatively affects fructification (Hayatu & Mukhtar, 2014). Besides, drought stress induces the accumulation of malondialdehyde (MDA), an oxidative stress biomarker; proline, sugars, and proteins (Moller et al., 2007; Farooq et al., 2009). Plants' responses to drought are complex (Carvalho et al., 2019); they use various mechanisms (avoidance, tolerance, etc.) to withstand drought stress (Blum et al., 2005). They increase root volume evenly to enhance water uptake (Farooq et al., 2009; Santos et al., 2020) or undergo a root volume reduction (Jaleel et al., 2009; Wach & Skowron, 2022) due to a slowdown in root neoformation. Although cowpea is drought-tolerant plant, short rains/irrigation can reduce its yield (Dadson et al., 2005).

MATERIALS AND METHODS

Plant Material

Seeds from six cowpea genotypes (Table 1) were used in this study, including five local and one introduced (TVX, an improved variety). They have been obtained from a collection of the Laboratoire de Physiologie et de Biotechnologies Végétales of Université de Lomé. They correspond to six different genotypes (Figure 1) and are among the most widespread in Togo (Dagnon, 2018). The seeds were treated with bleach (5%) and then thoroughly rinsed (twice) with distilled water before sowing.

Table 1: Characteristics of cowpea varieties studied

Varieties	Port	Cycle	Npo	Lpo	Yield	Area
Amélassiwa	Erected	69	30,95	17,54	765,03	Wli
Ketcheyi (Kpoyodji)	Erected	64	19,54	18,1	980,21	Akodessewa, Kassa
Ketcheyi-Soukpelo	Semi-erected	67	26,25	18,94	1179,69	Kassi
Malgbong-Bomoine	Semi-erected	67	31,75	19,19	943,75	Nagbeni
Siéloune	Erected	64	32,76	16,16	1341,67	Nagbeni
TVX	Erected	65	25,58	17,14	757,29	Périmètre (Ogou)

Npo: number of pods; Lpo: Length of the pods in cm; Yield in Kg/ha **Source:** Dagnon (2018).

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Figure 1: Cowpea varieties

Experimental Design

The experiment was carried out under semi-controlled conditions, in a plant growing compartment at the Station d'Expérimentations Agricoles (SEA) of the Université de Lomé between August and October 2022. Plants grew in 10-litre plastic vegetation pots with holes drilled to drain the water after watering. The device was a 3x2 split plot (three runs/repetitions; two treatments: control and stressed) with two interacting factors, varietal type and water regime. The experimental unit consisted of three pots for each treatment (control, stressed), for a total of 108 pots for the six varieties. Each pot was filled with 7 kg of substrate, consisting of the soil taken from the station and sifted to 2 mm, sterilized by heating, and then made up to 1/10 with compost (Ledi, 2020). The water deficit was induced by reducing irrigation from 70% of AWC (control) to 30% of AWC (stressed) (Bokobana et al., 2019; Ledi, 2020) in the flowering phase, known as the most susceptible phase to drought. Plants were watered by sequentially weighing the pots at 3-day intervals, bringing the control pots to the same weight (70% of the AWC), while the stressed plants underwent a water deficit at 30% of the AWC. The water deficit was applied for 14 days, which corresponds to the average duration of sudden drought during cropping cycles in Togo (Ledi, 2020). At the end of water deprivation, irrigation of the stressed plants was resumed as for the control plants, i.e., with 70% of the AWC. The average growth conditions in the greenhouse during the experiment were a photoperiod of 12 hours, an average ambient temperature 27.67°C. The AWC was calculated using this formula (Baize, 2000):

$$AWC = (Wcc\ 2{,}5 - Wpfp\ 4{,}2)\ x\ Da\ x\ E\ x\ Tfine$$

AWC: available water content (mm); Wcc 2.5: moisture weight at field capacity in percentage (%), Wpfp 4.2: moisture weight at permanent wilting point in percentage (%); Tfine: fine particle content, E: soil depth in the pot (dm), Da: bulk density of the soil (t.m-3).

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Determination of Physiological, Biochemical, and Agronomic Variable Fluctuations

During the experiment, the height of the plants (HTR) was measured and the number of leaves (NLE) counted, both every 7 days, mainly during water deprivation period (three times for 14 days of deprivation). At each time, the average value of each variable (HTR or NLE) was determined. On the last day of the water deprivation period, fresh leaf samples were collected in the morning for relative water content (RWC), proline content (PLN), total protein content (PROT), and malondialdehyde content (MDA) determination using the methods of Clarke et al. (1991) and Jones (2007) for RWC, Bogdanov et al. (1999) for PLN, Bradford (1976) for PROT, and Heath and Parker (1968) for MDA, respectively. Few hours later, pods were harvested, and the average number of pods per plant (NPO), the average pod length per plant (LPO), the average number of seeds per plant (NSD), and the average seed mass per plant (productivity) (PDV) were determined, as well as the average length of the main root (LRP) and the average number of lateral (secondary) roots (NRS) ≥ 2 cm.

Statistical Analysis

The data were processed with R software. First, a rank transformation was performed on non-Gaussian distribution variables (Holbert, 2022) after testing normality. Then, ANOVA was performed to determine the effects of each factor (water regime (WR) and varietal type (VRT)) on each variable. To elucidate the principal components of our variables and the distribution of varieties according to these ones, a PCA was also performed. The Tukey HSD test allowed for comparing variable means and elucidating those that contributed highly to the significance. The default significance threshold was 5%. To assess the correlations between the variables, Spearman's method was used. The change rate (S) in each variable was determined as follows:

$$S = \frac{Vs - Vc}{Vc} \; x\, 100$$

S: incidence of water deficit (Percentage of decrease or increase in the parameter); Vs: value of the stressed; Vc: value of the control.

The stress or drought susceptibility index (DSI) was calculated according to the formula of Fischer and Maurer (1978). A cultivar is considered as tolerant if its DSI is less than 1:

$$DSI = \frac{1 - Y}{D}$$

Y = Ys/Yc*. Ys: yield of a stressed cultivar;* ***Yc****: yield of non-stressed (control);* ***D = 1 - (Yms/Ymc)****.* ***D****: drought intensity;* ***Yms****: mean of the yields of stressed varieties;* ***Ymc****: mean of the yields of non-stressed.*

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RESULTS

Analysis of Variance Results

Analysis of variance revealed a significant effect ($p < 0.05$) of drought stress on physiological and agronomic parameters (Tables 2 and 3), except for the variable LRP (main root length). For biochemical markers, there was a significant effect of water deficit on MDA levels; no effect was observed for total protein and proline levels ($p > 0.05$). However, at a confidence interval of 70%, the effect was significant for proline content. The analysis also revealed a significant effect ($p < 0.05$) of varietal type on all measured variables (physiological, biochemical, and agronomic) (Tables 2 and 3), but the interactions of both factors (VRT: WR) were only significant ($p < 0.05$) for the number of leaves and the proline content.

Table 2: Analysis of variance of physiological and biochemical variables

	Df	HTR	NLE	RWC	Protein	Proline	MDA
Varieties	5	4.2e-10***	1.89e-08 ***	0.00444 **	8.9e-06 ***	6.25e-06 ***	0.000613 ***
WR	1	0.000157***	0.000651 ***	0.01392 *	0.5032 **ns**	0.294843 **ns**	0.038045*
Interaction	5	0.095871 **ns**	0.048104 *	0.62904 **ns**	0.0684 **ns**	9.89e-06 ***	0.755421 **ns**
Residuals	24						

Signif. Codes 0‘***’; 0.001‘**’ ; 0.01‘*’ **ns** : not significant

***Df**: degree of freedom.*

***Parameters**: **WR**: water regime; **HTR**: plant height; **NLE**: average number of leaves per plant; **RWC**: relative water content; **MDA**: malondialdehyde.*

Table 3: Analysis of variance of agronomic variables

	Df	NRS	LRP	NPO	LPO	NSD	PDV	YIELD
Varieties	5	0.00367 **	0.326 **ns**	3.93e-05***	6.22e-06 ***	8.14e-05***	1.35e-08 ***	0.00365**
WR	1	0.02988 *	0.518 **ns**	0.0104*	0.0374 *	0.0232*	0.0162 *	0.03873 *
Interaction	5	0.71346 **ns**	0.807 **ns**	0.8321 **ns**	0.6738 **ns**	0.9646 **ns**	0.2174 **ns**	0.79910 **ns**
Residuals	24							

Signif. Codes 0‘***’ ; 0.001‘**’ ; 0.01‘*’ ; **ns** : not significant

***Df**: degree of freedom.*

***Parameters**: **WR**: water regime; **NRS**: average number of lateral roots* ≥ 2 cm*; **LRP**: average length of the main root; **NPO**: average number of pods per plant; **LPO**: average pod length; **NSD**: average number of seeds per plant; **PDV**: average productivity.*

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Effect of Water Deficit on Physiological and Biochemical Parameters

RWC, leaf count, and plant height all decreased as a result of the water deficit. RWC decreased by 0.5% in the cultivar TVX, 5.64% in Ketcheyi, 9% in Amélassiwa, and 9.07% in Siéloune. This loss resulted in stunted growth, with a reduction in the number of leaves of 1.72% in Malgbong-Bomoine, 5.75% in Ketcheyi-Soukpelo, 19.44% in Ketcheyi, and 21.65% in Amélassiwa. Regarding the average height of the plants, there was a growth decline of 0.8% in Siéloune, 25.86% in Malgbong-Bomoine, 35.18% in Ketcheyi-Soukpelo, and 42.08% in Ketcheyi. For RWC and NLE variables, Ketcheyi-Soukpelo and Malgbong-Bomoine **(Table 4: Figures A, B, C)** exhibited similar responses each time, significantly.

The data also revealed a non-significant effect of water deficit on the main root growth, despite the increases in average main root length of about 11% in Ketcheyi, Malgbong-Bomoine, Siéloune, 1.95% in Amélassiwa, and the decreases of about 9% in Ketcheyi-Soukpelo and 2.71% in TVX. For this variable, responses were not significantly different **(Table 4: Figure D)**. However, there was a significant halt in lateral roots in all varieties, with higher reductions in Ketcheyi and Ketcheyi-Soukpelo of 39.91% and 27.4%, respectively. Siéloune's response was significantly different from others **(Table 4: Figure E)**.

Regarding biochemical markers, Ketcheyi-Soukpelo, Malgbong-Bomoine, and TVX showed an increase of 8%, 105.46%, and 329.77% in protein content, associated with a decrease in proline content of 11.52%, 67.91%, and 79.91%, respectively. In contrast, Amélassiwa, Ketcheyi, and Siéloune showed a decrease in protein content of 31.48%, 20.32%, and 34.62%, combined with an increase in proline content of 30.97%, 121.10%, and 30.37%, respectively. The effect on both was not significant. Thus, for protein content, TVX (improved variety) showed higher protein accumulation than others, while Ketcheyi and Siéloune responded similarly **(Table 4: Figure F)**. For proline contents, the trio —Ketcheyi, Ketcheyi-Soukpelo and Malgbong-Bomoine— exhibited similar responses that were significantly different from Amélassiwa, Siéloune and TVX. **(Table 4: Figure G)**.

For MDA content, results revealed a significant accumulation in all varieties with a peak in Amélassiwa (56, 56%), except in Ketcheyi-Soukpelo, where it was zero. Malgbong-Bomoine and TVX showed responses significantly different from others and from each other **(Table 4: Figure H)**.

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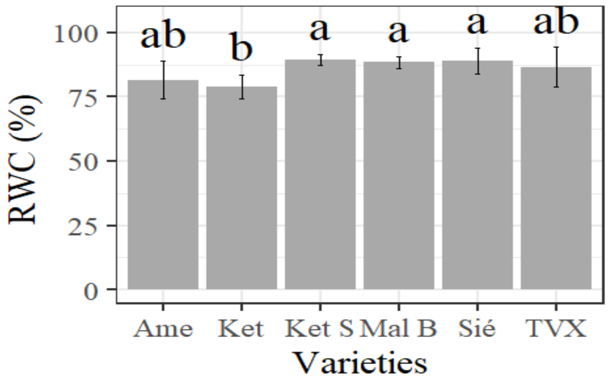
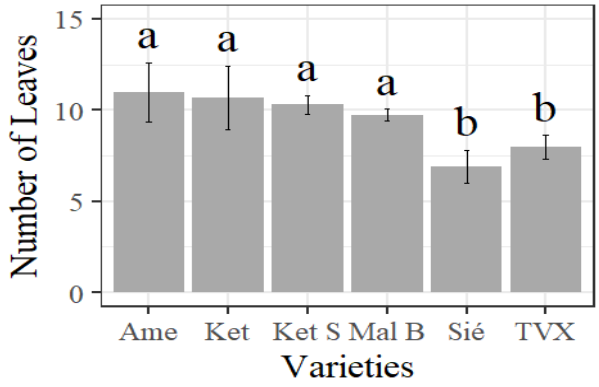
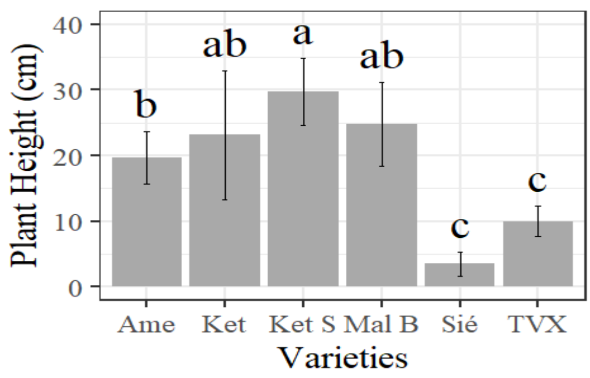
Table 4: Effect of water deficit on physiological and biochemical variables (means comparison, Tukey HSD)



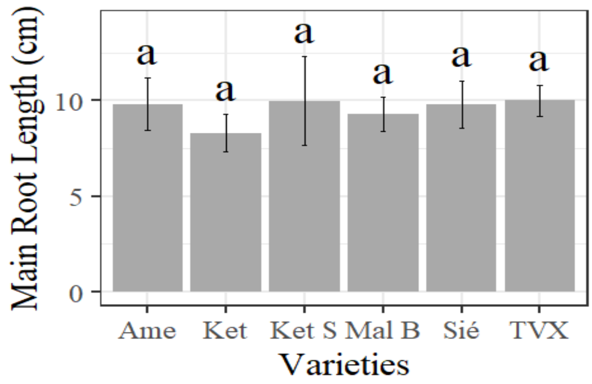
A. Relative water content (RWC)
(*pval-vrt <0.05; pval-wr <0.05; pval-vrt:wr >0.05*)



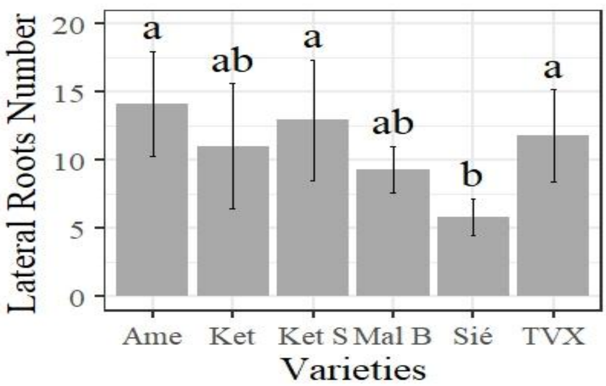
B. Average number of leaves
(*pval-vrt <0.05; pval-wr <0.05; pval-vrt:wr <0.05*)



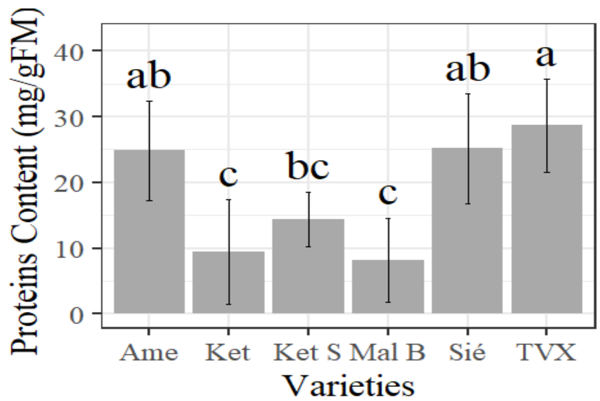
C. Plant height
(*pval-vrt <0.05; pval-wr <0.05; pval-vrt:wr >0.05*)



D. Main root length
(pval-vrt >0.05; pval-wr >0.05; pval-vrt:wr >0.05)



E. Lateral roots number
(*pval-vrt >0.05; pval-wr >0.05; pval-vrt:wr >0.05*)



F. Proteins content
(pval-vrt <0.05; pval-wr >0.05; pval-vrt:wr >0.05)

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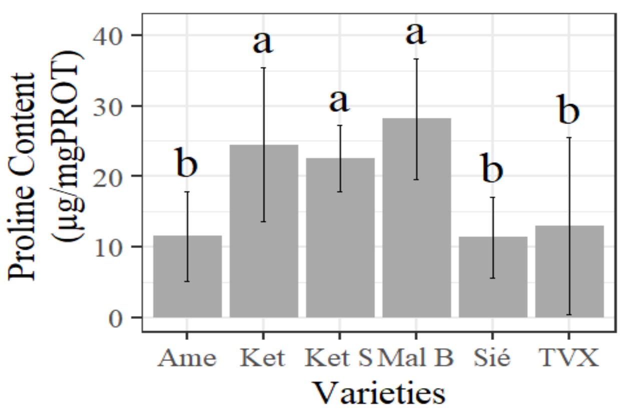
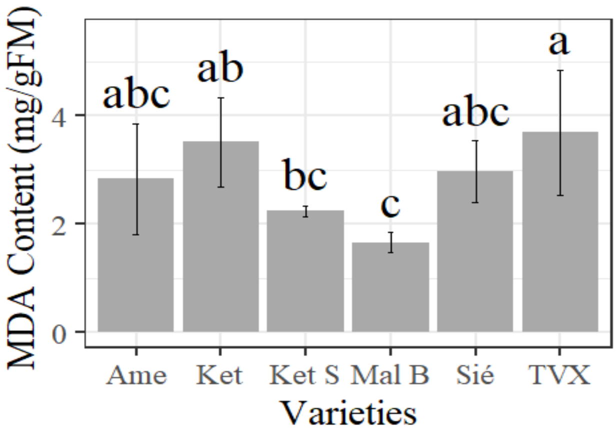


G. Proline content
(pval-vrt <0.05; pval-wr >0.05; pval-vrt:wr <0.05)



H. MDA (Malondialdehyde) content
(pval-vrt <0.05; pval-wr <0.05; pval-vrt:wr >0.05)

Legend (Table 4): ***pval-vrt*** *= p-value of varieties effect,* ***pval-wr*** *= p-value of water regime effect;* ***pval- vrt:wr*** *= interaction p-value. Varieties with the same letter are not significantly different.* ***Ame****: Amélassiwa,* ***Ket S****: Ketcheyi-Soukpelo,* ***Ket****: Ketcheyi,* ***Mal B****: Malgbong-Bomoine,* ***Sié****: Siéloune.* ***FM***: Fresh matter.

Effect of Water Deficit on Agronomic Parameters

The water deficit induced significant decreases in the number and length of pods and in the number of seeds, productivity, and plant yield. The average number of pods decreased by about 60.24% in Amélassiwa and 100% in Ketcheyi (no fruiting), while the average pod length decreased by about 47.05% in Amélassiwa and 43.41% in Ketcheyi-Soukpelo. There was also a sharp drop in the number of seeds per plant of 69.87% in Amélassiwa and 41.93% in TVX. Therefore, TVX and Amélassiwa experienced a decline in productivity of about 27.79% and 70.02%, respectively, and in yield approximately 29.78% and 70.12%, respectively. Thus, for NPO, LPO, NSD and yield variables, Ketcheyi-Soukpelo, Malgbong-Bomoine, Siéloune and TVX, each time, exhibited similar responses not significantly different **(Table 5: Figures I, J, K, K, L, M).** The average number of pods, length of pods and number of seeds values of the variety Ketcheyi were significantly different from other varieties' values. **A**nalysis of DSIs (Fisher-Maurer indexes) revealed that Ketcheyi-Soukpelo, Malgbong-Bomoine, Siéloune and TVX are drought-tolerant (DSIs < 1), while Amélassiwa and Ketcheyi are susceptible (DSIs > 1).

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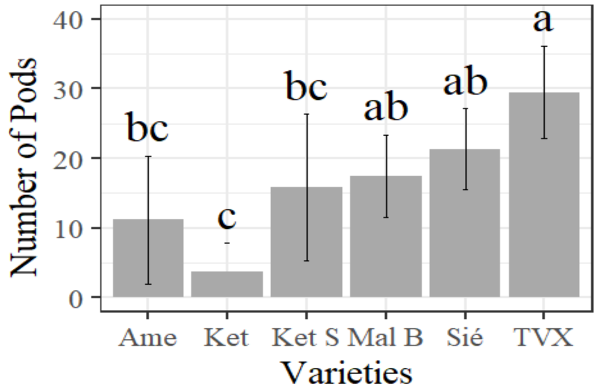
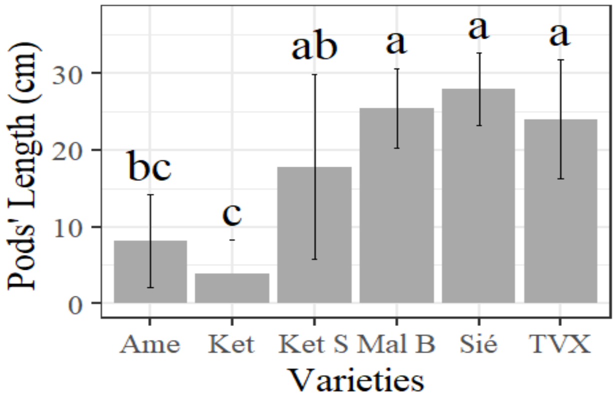
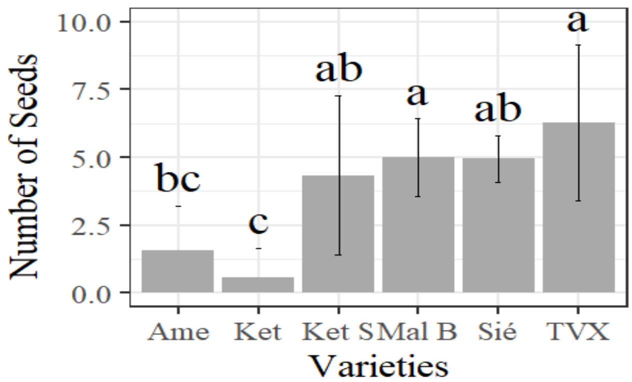
Table 5: Effect of water deficit on agronomic variables (means comparison, Tukey HSD)



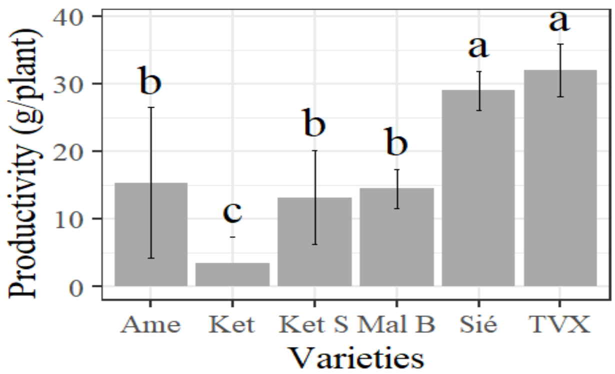
I. Average number of pods
(pval-vrt <0.05; pval-wr <0.05; pval-vrt:wr >0.05)



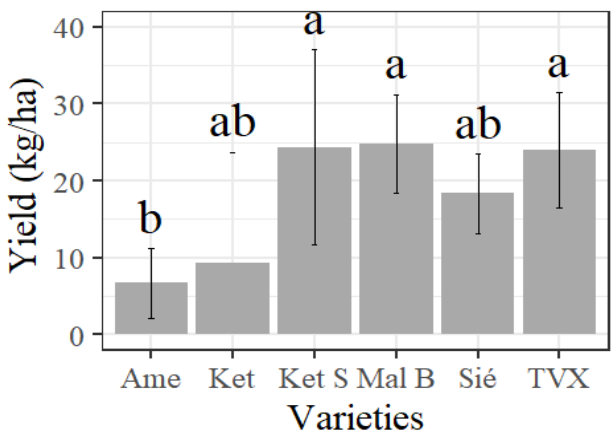
J. Average length of pods
(pval-vrt <0.05; pval-wr <0.05; pval-vrt:wr >0.05)



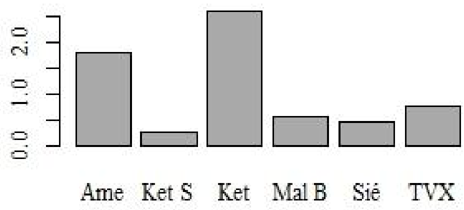
K. Average number of seeds
(pval-vrt <0.05; pval-wr <0.05; pval-vrt:wr >0.05)



L. Average Productivity
(pval-vrt <0.05; pval-wr <0.05; pval-vrt:wr >0.05)



M. Varieties' average yields
(pval-vrt <0.05; pval-wr <0.05; pval-vrt:wr >0.05)



N. Drought susceptibility indexes (DSI)

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Legend (Table 5): ***pval-vrt*** *= p-value of varieties effect;* ***pval-wr*** *= p-value of water regime effect;* ***pval-vrt:wr*** *= interaction p-value. Varieties with the same letter are not significantly different.* ***Ame****: Amélassiwa,* ***Ket S****: Ketcheyi-Soukpelo,* ***Ket****: Ketcheyi,* ***Mal B****: Malgbong-Bomoine,* ***Sié****: Siéloune.*

Spearman Correlation Between the Variables

The analysis confirmed a negative correlation between protein and proline contents (**Figure 2**). MDA was negatively correlated with plant height, number of leaves, RWC and proline content, but positively connected with protein content. Plant productivity was negatively correlated with average height and number of leaves, which was negatively correlated with all yield variables. The number of lateral roots was positively correlated with average plant height and number of leaves, and negatively correlated with RWC. Finally, yield parameters were positively correlated with each other.

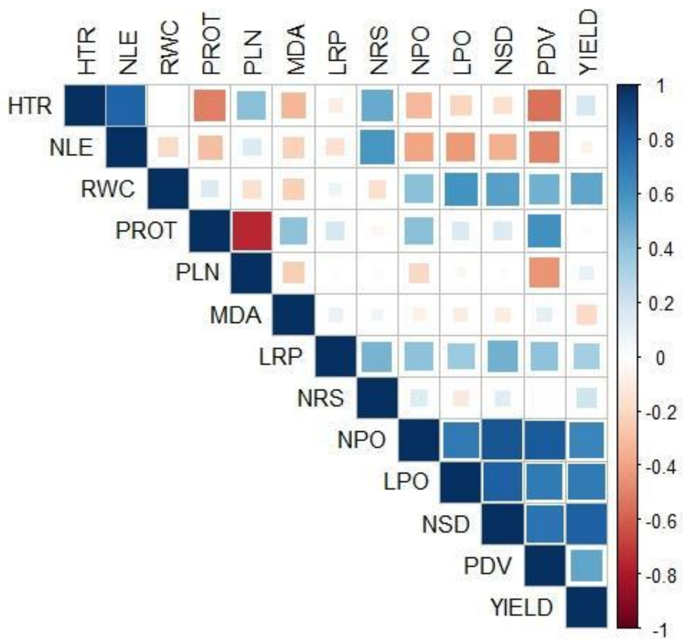

Figure 2: Correlation matrix visualisation

Legend: ***HTR****: height;* ***NLE****: mean number of leaves;* ***RWC****: relative water content;* ***PROT****: total proteins;* ***PLN****: Proline;* ***MDA****: malondialdehyde;* ***LRP****: average main root length;* ***NRS****: Mean number of lateral roots ≥ 2cm;* ***NPO****: mean number of pods;* ***LPO****: average pod length;* ***NSD****: mean number of seeds;* ***PDV****: average productivity.*

Principal Component Analysis

Principal component analysis revealed that the initial two axes accounted for approximately 60.81% of the information and, when joined with the third dimension, elucidated 74.38% of the information. Yield variables exhibited a correlation with the first axis, while biochemical variables were more associated with the second axis. Two major groups emerged from the first two axes. The first group consists of Amélassiwa, which is negatively connected to the first axis; Ketcheyi, which is negatively connected to both axes on the one hand; and Ketcheyi-

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Soukpelo and Malgbong-Bomoine, which are both more connected to the second axis and proline content on the other. The second group consisted of TVX and Siéloune, positively correlated with both axes and with protein and MDA contents. Therefore, varieties exhibiting higher yields were more connected with proline content, whereas those showing higher productivity were more correlated with protein and MDA contents. Morphophysiological parameters (HT, NLE, NRS) are negatively correlated with both axes.

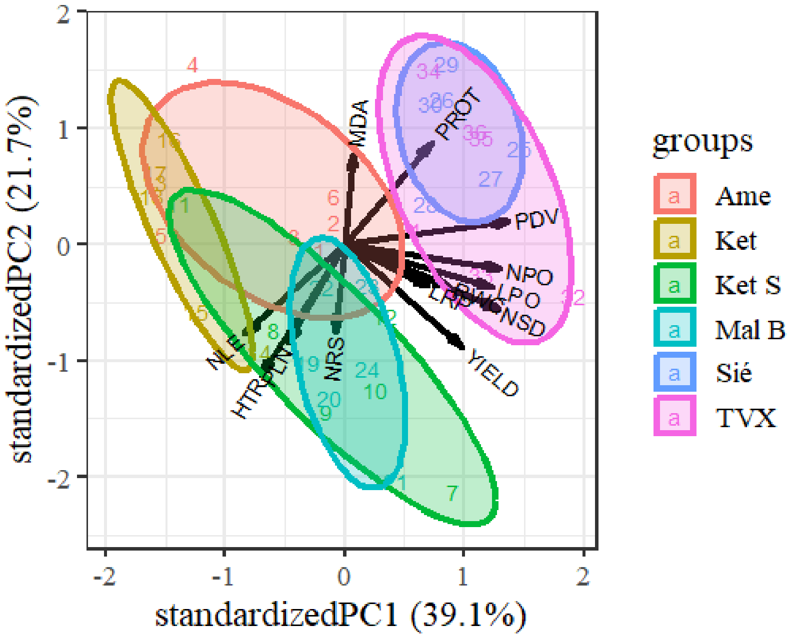

Figure 3: Projection of all variables along the first two dimensions

Legend: ***HTR***: *height;* ***NLE***: *mean number of leaves;* ***RWC***: *relative water content;* ***PROT***: *total proteins;* ***PLN***: *Proline;* ***MDA***: *malondialdehyde;* ***LRP***: *average main root length;* ***NRS***: *Mean number of lateral roots ≥ 2cm;* ***NPO***: *mean number of pods;* ***LPO***: *average pod length;* ***NSD***: *mean number of seeds;* ***PDV***: *average productivity.* ***Ame***: *Amélassiwa;* ***Ket S***: *Ketcheyi-Soukpelo;* ***Ket***: *Ketcheyi;* ***Mal B***: *Malgbong-Bomoine;* ***Sié***: *Siéloune.*

DISCUSSION

The six examined varieties exhibited various decline rates in RWC. Amélassiwa and Ketcheyi exhibited moderate stress while Ketcheyi-Soukpelo, TVX, Malgbong-Bomoine, and Siéloune showed mild stress. With greater decreases in RWC, Amélassiwa and Siéloune were more affected. The larger declines in HTR in Ketcheyi, Ketcheyi-Soukpelo, and Malgbong-Bomoine and in NLE in Amélassiwa and Ketcheyi elucidated greater growth inhibition in both of these varieties. They exhibited more susceptibility regarding these three variables. The growth inhibition affected root differentiation as well, leading to a decrease in the number of lateral roots ≥ 2 cm. Drought stress generally results in the inhibition of organogenesis in plants. Several studies reported similar declines in RWC (Kardile et al., 2018) and plant growth (Olorunwa et al., 2021; Atakora et al., 2023). For a 14-day induced water deficit, Thuc et al. (2022) also noticed a decrease in root growth in cowpea.

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Under drought stress, plants accumulate various molecules/solutes to achieve osmotic adjustment, close the stomata, or neutralise ROS, reactive oxygen species (Osakabe et al., 2014; Meena et al., 2019). Even if ANOVA revealed a non-significant effect of water deprivation on total protein and proline contents, the observed negative correlation between both contents could indicate two mechanisms to regulate their contents: protein degradation in Amélassiwa, Ketcheyi and Siéloune to liberate proline for an osmotic adjustment and, conversely, proline mobilisation in TVX, Malgbong-Bomoine and Ketcheyi-Soukpelo for the synthesis of proteins, such as multifunctional proline-rich proteins (PRPs) (Kavi Kishor et al., 2015; Ribeiro et al., 2023) and antioxidant system enzymes (CAT, APX, POD, etc.) (Ramalho et al., 2018 ; Bokobana et al., 2019). Therein, Gujjar et al. (2018) found a negative association between protein gene expression (PRPs) and proline levels in tomatoes during drought stress, implying that these proteins regulate proline levels. Carvalho et al. (2019) found a significant accumulation of proline in their work, and noticed that proline and anthocyanin contents have contributed mostly to discriminate genotypes under the water deprivation they imposed. Hamidou et al. (2007) also found a significant accumulation of proline with non-significant variation in protein content. Regarding MDA accumulation, it differed between varieties because the susceptibility to water deprivation is variety-dependent (Ndiso et al., 2016). The absence of accumulation of MDA in Ketcheyi-Soukpelo highlighted an effective strategy to maintain membrane integrity. Thus, the high accumulation in Amélassiwa revealed that the variety is the most susceptible. The other varieties showed intermediate values, meaning moderate susceptibility.

Water deficit often severely affects yield variables during the reproductive phase (Daryanto et al., 2015; Ngompe Deffo et al., 2024). The decrease in NSD and NPO in all varieties can be explained by a negative effect of water deficit on seed filling, pod formation, fertilisation, and photosynthesis, as mentioned by Farooq et al. (2009) and Hayatu and Mukhtar (2014). Besides, the negative correlation between the average number of leaves and yield variables elucidated a significant impact of the leaf area on these decreases. Of the six varieties studied, Amélassiwa and Ketcheyi were characterised by higher DSIs, indicating higher susceptibility to drought stress. According to varieties DSIs and PCA, the six varieties can be divided into three categories: susceptible varieties (Ketcheyi and Amélassiwa), medium-tolerant varieties (Siéloune, Malgbong-Bomoine, and TVX), and high-tolerant varieties (Ketcheyi-Soukpelo). PCA revealed as well that varieties that exhibited higher yields were correlated with proline content, while those that showed higher productivity and MDA level were correlated with protein content. TVX, an improved variety, had the highest protein content, a positive connection with MDA, and a DSI heading towards 1; this suggests that it may grow more susceptible to harsher droughts. Thus, based on this study and earlier research (Carvalho et al., 2019, dos Santos et al., 2022; de Souza Leite et al., 2023 etc.), osmotic adjustment mechanisms appear to be an important factor to examine first in varietal improvement.

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CONCLUSION

In all varieties examined, drought stress affected organogenesis negatively (decreases in plant height, number of leaves, lateral roots and fructification). A negative correlation between proline and protein contents was noted. This may elucidate some attempts to regulate these biochemical variables. Besides, an accumulation of MDA in all varieties was recorded except in Ketcheyi, but with a peak in Amélassiwa. Regarding yield parameters, each variety recorded a decline, with Amelassiwa and Ketcheyi recording the largest ones. These two varieties also exhibited very high DSIs, reflecting their high susceptibility to drought. With the lowest DSI, Ketcheyi-Soukpelo is the most tolerant variety, thereby a good candidate for a variety improvement programme that includes drought resistance. Cultivation of Amélassiwa and Ketcheyi varieties requires specific irrigation mechanisms well adapted to local agroecological conditions, especially during sudden drought periods. Finally, varieties that exhibited higher yields were correlated with proline content, whereas those showing higher productivity and MDA level were correlated with protein content. This implies that osmotic adjustments are important aspects to target first during variety improvement.

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