



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

Lamèga Madjonga^{*}, Atalaèssou Bokobana, Tchilabalo Ketetche, Yao Dodzi Dagnon, Outéndé Toundou, Damigou Bammite, and Koffi Tozo.

Laboratoire de Physiologie et de Biotechnologies Végétales, Faculté des Sciences, Université de Lomé (UL), 01 BP1515 Lomé 01, Togo.

^{*}Corresponding Author's Email: lamegahd@gmail.com

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ABSTRACT: Drought stress is a major hindrance to cowpea cultivation. Current 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 varieties grown in Togo. The experimental device, under semi-controlled conditions, was a split plot (three blocks, two treatments). 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 variables, total protein, proline, and malondialdehyde (MDA) levels, as well as yield variables, were determined, and the data were analyzed through ANOVA, Tukey's HSD, and principal component analysis (PCA) with R. The 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 deficit on physiological variables, except in principal root length (PR), total protein (PROT), and proline (PLN) contents ($p > 0.05$). However, a negative correlation between protein and proline contents was noted with a significant interaction on proline levels. Besides, the oxidative stress biomarker MDA was positively correlated with PROT. Regarding varieties' responses, the varietal type significantly influenced their responses, except in the PR variable. Leaf count (NLE) and DSIs contributed to discriminating varieties. PCA revealed that varieties that exhibited higher yields were often well centered on the first two principal components. 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, crop yield, drought tolerance, Togo.



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 beneficial source of protein, carbs, folate, vitamins, antioxidants, fiber, and other nutrients that help keep populations' diets balanced (Da Silva and da Costas Santos, 2019; Affrifah et al., 2022). 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 (Bado, 2002; Akissoé et al., 2021).

According to FAO (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 is fluctuating a lot, reflecting insufficient supply and production for a growing population and strong speculations. Besides, the yield per hectare is low. For several decades, Togo has been facing climatic fluctuations characterized 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, respectively, that the yield variables of the line IT98K-412-13 and the varieties VITOCO, VITA5, and IT87D-10-10 are significantly affected by water deficit. In their research, Manneh et al. (2024) identified six accessions that exhibited higher yields, with RK173 standing out as the best-performing accession under induced water deprivation. Currently, all promoted varieties in Togo (TVX, VITA5, VITOCO, NAFI SAM, and WANG-KAI) are improved ones that have been introduced due to their characteristics: high productivity, earliness, and resistance to *Striga* (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 the risk of renunciation and then disappearance of local varieties or varieties, of which Dagnon (2018) has characterized 70 genotypes. How do these characterized cowpea varieties respond to water deficits? In a context of climatic instabilities, it is necessary to identify valuable and performing varieties and set up plant resource conservation mechanisms. The purpose of this study is to evaluate stress responses in six short-cycle cowpea-characterized varieties grown in Togo by integrating some variables not mentioned in previous studies on cowpea in Togo, such as stress variables. Thus, identifying tolerant and susceptible varieties will contribute to breeding programs (for tolerant varieties) and an effective irrigation strategy (for susceptible varieties) by providing information on their adaptive mechanisms.

LITERATURE REVIEW

Water deficit refers to a state where the water available is insufficient to meet plants physiological needs, leading to stress often. Stress thresholds in the soil vary: for a water potential (Ψ) ranging from 0 to -0.3 MPa, plants are well-watered and feel no stress (Taiz et al., 2015); from -0.3 to -0.8 MPa, a mild stress is noticed, plants begin to close stomata (Kramer & Boyer, 1995); and from -0.8 to -1.5 MPa, a moderate to severe stress is noted



(Chaves et al., 2003) and a permanent wilting point ($\Psi < -1.5$ 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 $0.19 \text{ m}^3/\text{m}^3$. This value corresponds to about 30–35% of volumetric soil moisture. In leaves, for a relative water content (RWC) $> 90\%$, plants feel no stress; for RWC ranging from 80% to 90%, plants feel mild stress; from 70% to 80%, they feel moderate stress; and for an RWC $< 70\%$, a threshold for serious physiological dysfunction (Barrs & Weatherley, 1962; Jones, 2007), they undergo severe stress. Therefore, water deficit causes a slowdown in growth and negatively affects fructification and yield (Hayatu & Mukhtar, 2014; Ndiso et al., 2016). 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 cowpea-characterized varieties of the Laboratoire de Physiologie et de Biotechnologies Végétales (LPBV) of Université de Lomé (UL). They correspond to six different genotypes (**Figure 1**) more productive (Dagnon, 2018) and are among the most widespread in Togo. 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	Np	Lp	Yield	Area
Amélassiwa	Erected	69	30,95	17,54	765,03	Wli
Ketcheyi	Erected	64	25,51	18,35	1174,26	kawa
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)

Np: number of pods; *Lp*: Length of the pods in cm; Yield in Kg/ha (Dagnon, 2018).



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 replications; two treatments: control and stressed) with two interacting factors, varietal type (VT) and water regime (WR). 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):

$$AWC = (W_{cc\ 2,5} - W_{pfp\ 4,2}) \times Da \times E \times T_{fine}$$

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

Determination of Physiological, Biochemical, and Agronomic Variable Fluctuations

During the experiment, the height of the plants (PH) 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 (PH 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. Pods were harvested, and the average number of pods per plant (NPO), the average pods' length per plant (LPO), the average number of seeds per plant (NSD), and the average mass of seeds per plant or productivity (PDV) were determined, as well as the average length of the main root (PR) and the average number of lateral (secondary) roots (LR) ≥ 2 cm.

Statistical Analysis

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

$$S = \frac{Vs - Vc}{Vc} \times 100$$

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

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

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

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

RESULTS

Analysis of Variance Results

Analysis of variance (ANOVA) revealed a significant effect ($p < 0.05$) of water deficit on morphophysiological and agronomic variables (**Table 2**), except in PR. For biochemical markers, there was a significant effect of water deficit on MDA levels; no effect was noted for total protein and proline levels ($p > 0.05$). The analysis also revealed a significant effect ($p < 0.05$) of the varietal type on all variables (**Table 2**), except in PR as well; however, the interactions between varietal type and water deficit (VR x WR) were significant ($p < 0.05$) only for the count of leaves (NLE) and the proline content (PLN).

**Table 2: Results of ANOVA on assessed variables**

Variable	TF	p_VT	p_WR	p_VT_x_WR	Sig_VT	Sig_WR	Sig_VTxWR
RWC		0.0044	0.0139	0.629	***	***	ns
NLE		0	7.00E-04	0.0481	***	***	***
PH	RT	0	2.00E-04	0.0959	***	***	ns
PR		0.3263	0.518	0.8071	ns	ns	ns
LR		0.0037	0.0299	0.7135	***	***	ns
PROT	RT	0	0.5032	0.0684	***	ns	ns
PLN	RT	0	0.6147	0	***	ns	***
MDA		6.00E-04	0.038	0.7554	***	***	ns
NPO	RT	0	0.0104	0.8321	***	***	ns
LPO	RT	0	0.0374	0.6738	***	***	ns
NSD	RT	1.00E-04	0.0232	0.9646	***	***	ns
PDV	RT	0	0.0162	0.2174	***	***	ns
YIELD	RT	0.0037	0.0387	0.7991	***	***	ns

VT: varietal type; WR: water regime; RWC: relative water content; NLE: average number of leaves per plant; PH: plants' average height; PR: average length of the principal root; LR: average count of lateral roots ≥ 2 cm; PROT: Total protein content; PLN: Proline content; MDA: malondialdehyde content; NPO: average count of pods per plant; LPO: pods' average length; NSD: average count of seeds per plant; PDV: average mass of seeds per plant or productivity. TF: type of transformation; RT: rank transformation (Variables with no transformation are left blank.). ns: not significant

Effects of Water Deficit and Varietal Type

RWC, leaf count (NLE), plant height (PH), and lateral root count (LR) all decreased significantly under a moderate effect (RWC, NLE, and LR) and mild effect (PH) of water deprivation. Stressed plants exhibited declines of 5.1% in RWC, 8.3% in NLE, 39.5% in PH, and 24% in LR (**Figures 2. A, B, C, D**). Regarding MDA contents, stressed plants showed a significant accumulation of 33.5% (**Figure 2.E**). For yield variables, significant declines of 8.6% in LPO, 14.2% in NPO, 16.7% in NSD, 41.6% in YIELD, and 80% in PDV were noted (**Figure 2. F, G, H, I, J**).

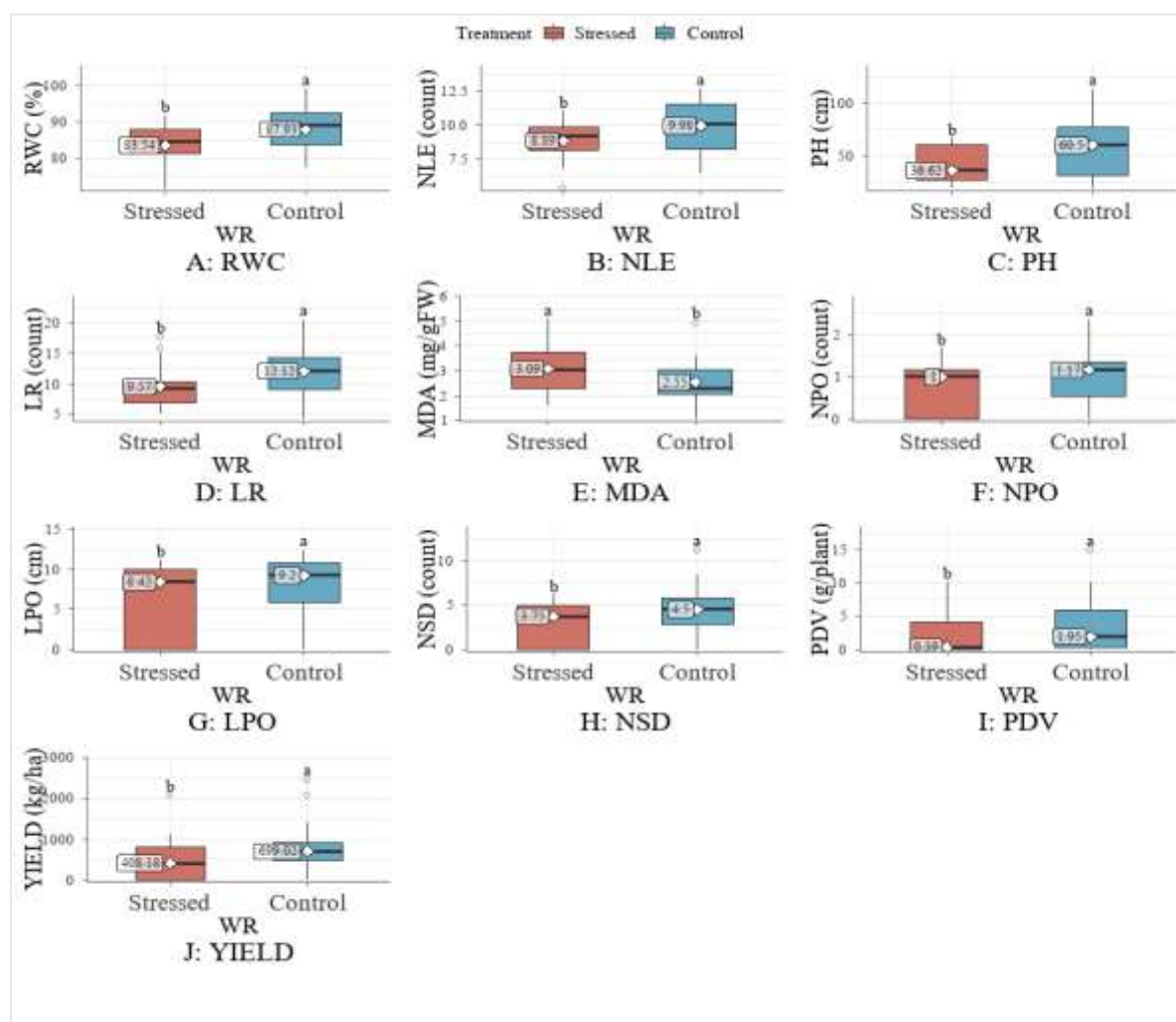


Figure 2. Effects of water deficit: significant cases

WR: water regime; **RWC:** relative water content; **NLE:** average number of leaves per plant; **PH:** plants' average height; **PR:** average length of the principal root; **LR:** average count of lateral roots ≥ 2 cm; **MDA:** malondialdehyde content; **NPO:** average count of pods per plant; **LPO:** pods' average length; **NSD:** average count of seeds per plant; **PDV:** average productivity.

The varietal type induced significant variations across the six varieties regardless of the effect of water deprivation. The greater interquartile (Q1-Q2) range observed in PH, MDA, NPO, LPO, NSD, and YIELD suggests that varieties' responses were disparate in these variables and more homogenous in the others. Under the induced water deprivation, RWC decreased by 9.56% in Amélassiwa and 9.07% in Siéloune; NLE decreased by 19.44% in Ketcheyi and 21.65% in Amélassiwa; PH decreased by 35.18% in Ketcheyi-Soukpelo and 42.08% in Ketcheyi; LR decreased by 39.91% and 27.4% in Ketcheyi and Ketcheyi-Soukpelo, respectively. 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. For MDA contents, results revealed a significant accumulation in all varieties with a peak in Amélassiwa (56.56%), except in Ketcheyi-Soukpelo, where the fluctuation was about 0%. Besides these effects, the water deprivation caused significant decreases in NPO, LPO, NSD, productivity (PDV), and plant yield, with a mild effect each time. NPO decreased by 60.24% in Amélassiwa and 100% in Ketcheyi (no fruiting), while LPO decreased by 47.05% in Amélassiwa and 43.41% in Ketcheyi-Soukpelo. There was also a sharp drop in NSD of 69.87% in Amélassiwa and 41.93% in TVX. Then, Amélassiwa experienced the highest decline in productivity, about 70.02%, while its crop yield exhibited a drop of about 70.12%.

Despite these decreases, the effect of water deficiency was not significant across varieties in several situations (except in NLE and PLN), as evidenced by non-significant interactions.

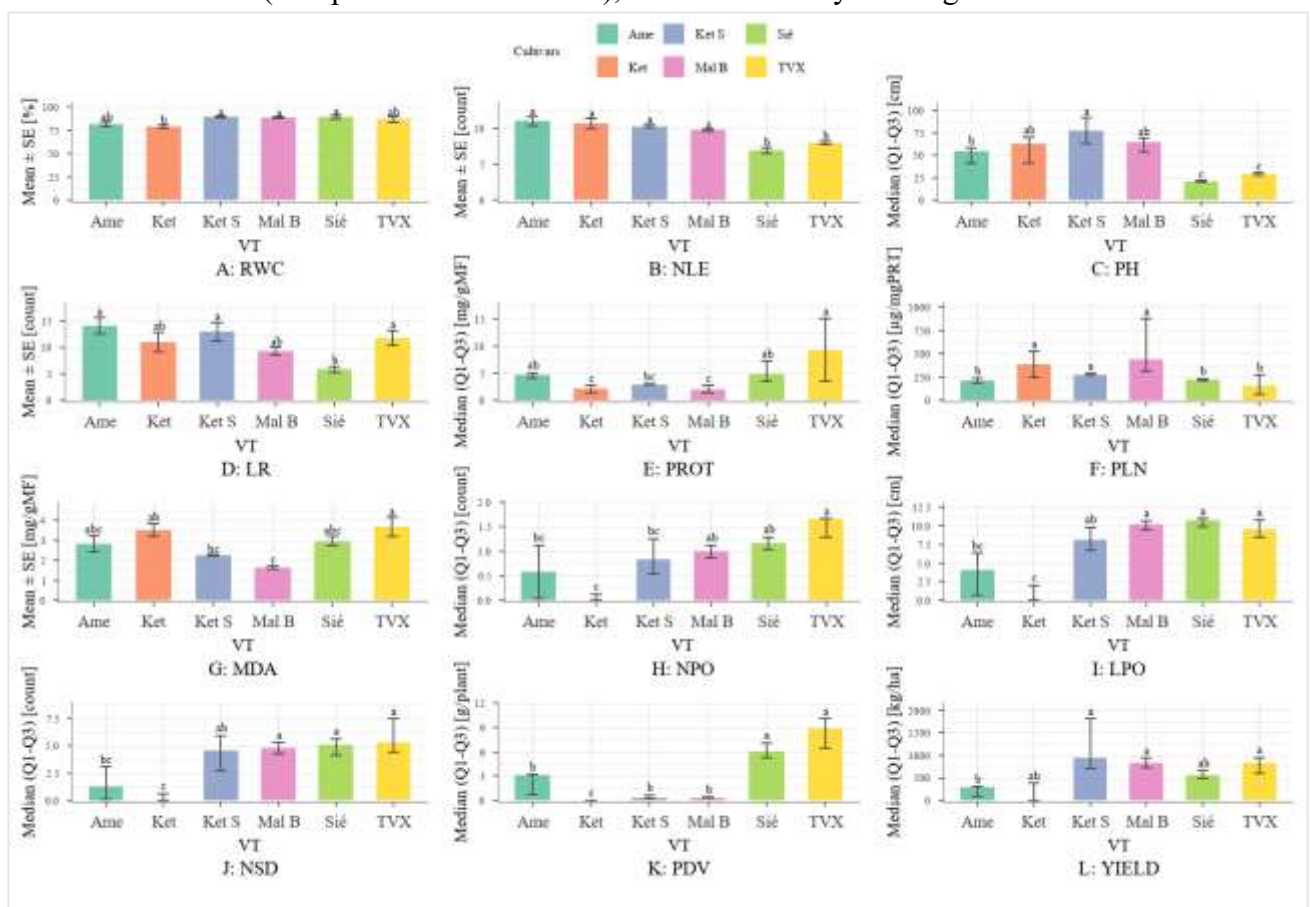


Figure 3: Effect of varietal type: significant cases

Some varieties exhibited similar declines. For example, in RWC and PH variables, Amélassiwa and TVX (**Figure 3.A**), on one hand, and Ketcheyi and Malgbong-Bomoine (**Figure 3.C**), on the other, exhibited similar decreases, respectively. However, for PLN and NLE, varieties showed different responses significantly (p -interaction < 0.05). Therefore, the significant effect of water deficit on variables was globally homogenous among varieties.

VT: Varietal type; **Varieties:** **Ame:** Amélassiwa, **Ket S:** Ketcheyi-Soukpelo, **Ket:** Ketcheyi, **Mal B:** Malgbong-Bomoine, **Sié:** Siéloune. Varieties with the same letter are not significantly different. **Variables:** **RWC:** relative water content; **NLE:** average number of leaves per plant; **PH:** plants' average height; **LR:** average count of lateral roots ≥ 2 cm; **PROT:** Total protein



content; **PLN**: Proline content; **MDA**: malondialdehyde content; **NPO**: average count of pods per plant; **LPO**: pods' average length; **NSD**: average count of seeds per plant; **PDV**: average productivity. **-Units: FW**: fresh weight. For variables whose distributions were not normal (non-Gaussian), the median (stronger) was used instead of the mean.

The analysis of the Fisher-Maurer indexes (Drought Susceptibility Indexes) revealed that Ketcheyi-Soukpelo, Malgbong-Bomoine, Siéloune and TVX are drought-tolerant (DSIs < 1), while Amélassiwa and Ketcheyi are susceptible (DSIs > 1) (**Figure 4**).

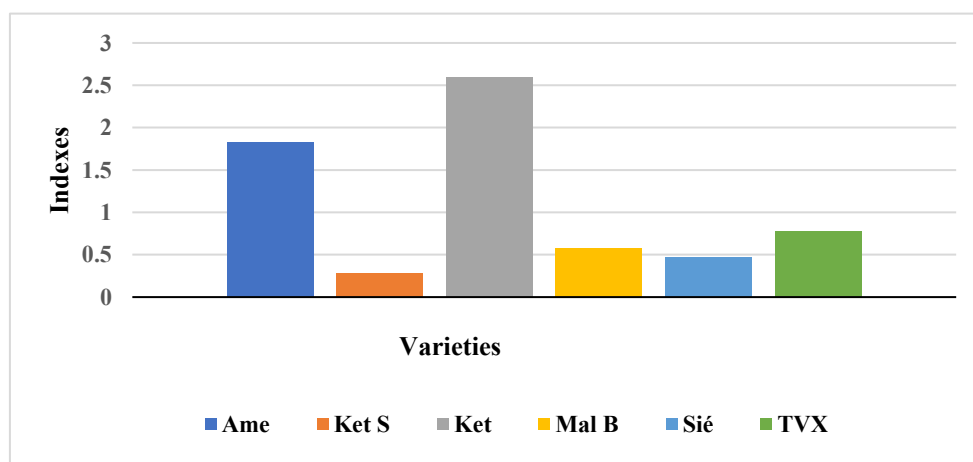


Figure 4: Varieties' DSIs

Varieties: *Ame*: Amélassiwa, *Ket S*: Ketcheyi-Soukpelo, *Ket*: Ketcheyi, *Mal B*: Malgbong-Bomoine, *Sié*: Siéloune. **DSIs**: Drought Susceptibility Indexes.

Spearman Correlation between the Variables

The test revealed a negative correlation between protein and proline contents. MDA was negatively correlated with average plant height (PH), average number of leaves (NLE), RWC, and proline content but positively with protein content. Plant productivity (PDV) was negatively correlated with PH and NLE; the latter were negatively correlated with yield variables (LPO, NPO, PDV, and NSD). The number of lateral roots (LR) was positively correlated with PH and NLE and negatively correlated with RWC, which was positively correlated with all yield variables (**Figure 5**).

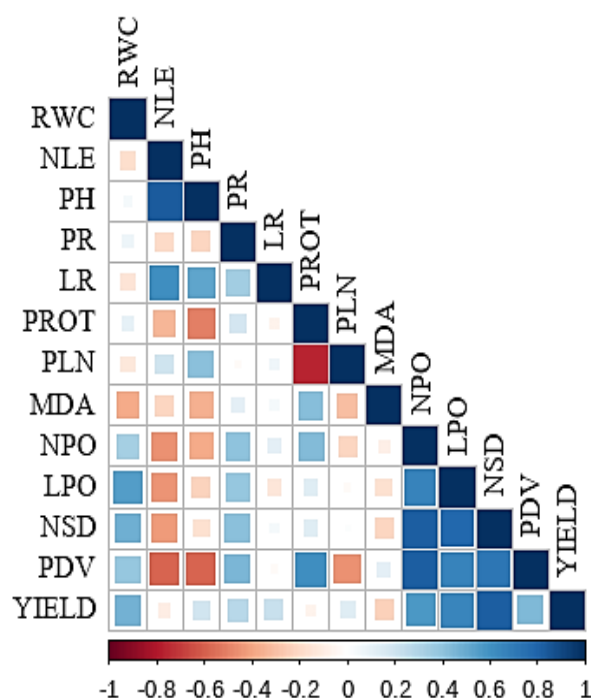


Figure 5: Matrix of spearman correlation

PH: height; *NLE*: mean number of leaves; *RWC*: relative water content; *PROT*: total proteins; *PLN*: Proline; *MDA*: malondialdehyde; *PR*: average main root length; *LR*: Mean number of lateral roots $\geq 2\text{cm}$; *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 first two axes accounted for approximately 57,6 % of the information (**Figure 6. A**) and, when joined with the third dimension, elucidated 71,6 % of the information. Yield variables exhibited a correlation with the first axis, while biochemical variables were more associated with the second axis (**Figure 6.A, B**). Both first axes exhibited overlapped varieties confirming the homogenous responses of varieties. The third source of variation (Dim3), with little contribution has further facilitated the distribution or discrimination of varieties (**Figure 6.B and C**). Three groups emerged from the analysis. The first group consists of Amélassiwa and Ketcheyi, which are often correlated with NLE and PH and widely negatively correlated with yield variables (**Figure 6.A and B**). The second group consists of Ketcheyi-Soukpelo and Malgbong-Bomoine, which are often well centered on both axes (**Figure 6.A and B**). The third group is formed by Siéloune and TVX, which are often more correlated with the first component (**Figure 6.A and B**). The analysis also revealed a strong correlation of Amélassiwa, Ketcheyi, and TVX with oxidative stress variables (MDA, PROT) which were opposed to growth and yield's variables (**Figure 6.C**).

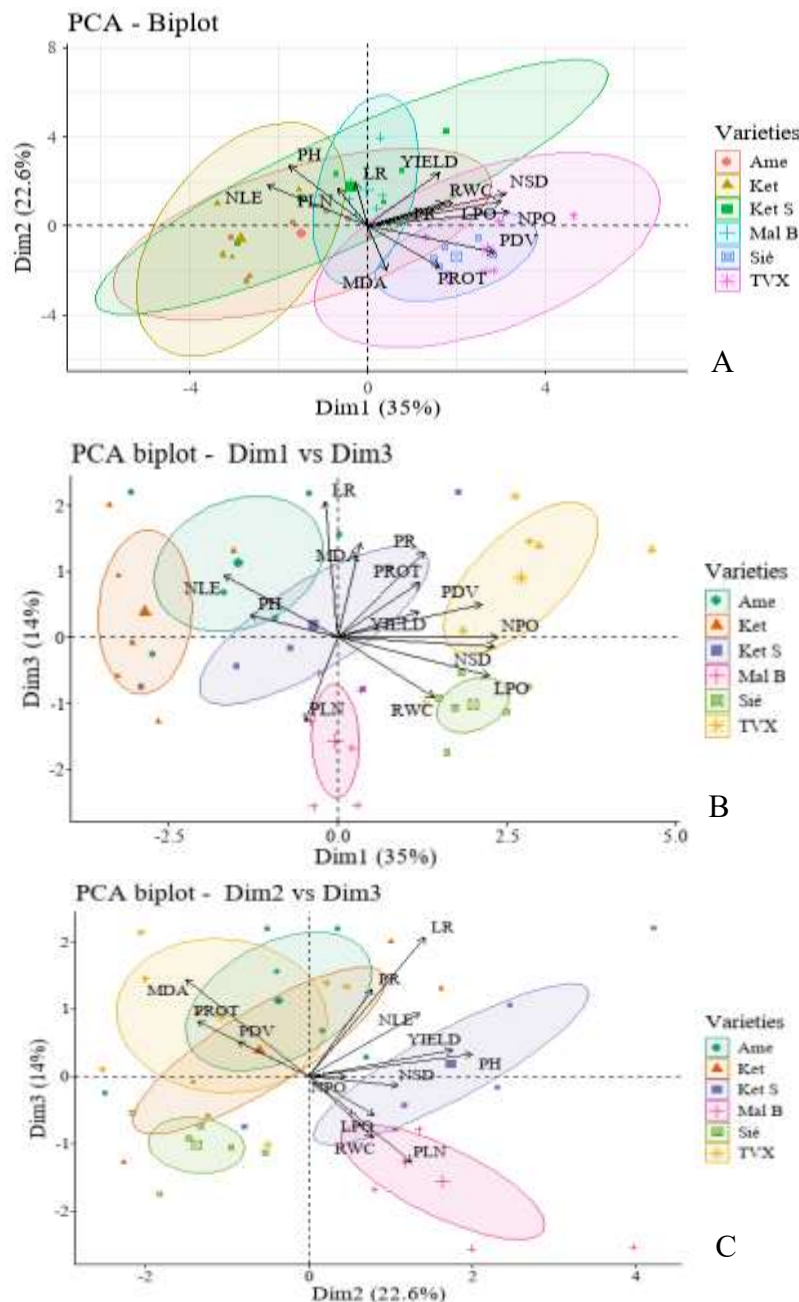


Figure 6. Projection of variables and varieties: Dim1 vs Dim 2 (A); Dim1 vs Dim3 (B) and Dim2 vs Dim3 (C)

PH: Plant height; **NLE:** mean number of leaves; **RWC:** relative water content; **PROT:** total proteins; **PLN:** Proline; **MDA:** malondialdehyde; **PR:** average main root length; **LR:** Mean number of lateral roots ≥ 2 cm; **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

In this study, the water deficit caused various significant effects on most of the variables, ranging from mild to moderate stress. In several cases, the interactions between both factors (VT and WR) were not significant, suggesting that the effect of the water deprivation was homogenous on varieties globally and revealing that these ones responded similarly to water deprivation.

The stressed plants exhibited various decline rates in RWC, NLE, and PH. Plants' growth relies on their water status. The reduction in RWC often leads to a decline in leaf turgor and in growth. Therefore, the drop in RWC led to a growth inhibition that elucidates the significant declines in NLE and in PH. The inhibition affected root differentiation as well, leading to a significant decrease in the number of lateral roots ≥ 2 cm. 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. (2023) also noticed a decrease in root growth in cowpea. However, other authors noticed an increase in root volume. The significant effect of VT, WR, and their interaction on NLE makes this variable a discriminating parameter. These effects impacted yield's components. 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, fertilization, 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. The drop in LPO and in NPO resulted in a drop in the NSD due to the positive correlation between them. Even though varieties exhibited homogenous responses, the DSIs calculated conversely revealed that some varieties are drought-tolerant (Ketcheyi-Soukpelo, Malgbong-Bomoine, Siéloune, and TVX), while others (Amélassiwa and Ketcheyi) exhibit drought susceptibility due to their high DSIs above 1. Thus, DSI and NLE are the variables that contribute to discrimination in this study. According to DSIs, the six evaluated varieties can be divided into three categories: susceptible varieties (Ketcheyi and Amélassiwa), medium-tolerant varieties (Siéloune, Malgbong-Bomoine, TVX), and high-tolerant varieties (Ketcheyi-Soukpelo). These results confirm that a non-significant p-value at a certain fixed threshold is not always a synonym of a total absence of effect.

Under drought stress, plants accumulate various molecules, or solutes, to achieve an osmotic adjustment and maintain water status, close the stomata, or neutralize reactive oxygen species (ROS) resulting from oxidative stress (Osakabe et al., 2014; Meena et al., 2019). Even if ANOVA revealed a non-significant effect on total protein and proline contents, the effect of the interaction (VT x WR) was significant on proline content, suggesting that varieties responded significantly differently. Besides, the negative and strong correlation between both contents could indicate two attempts or possible mechanisms to regulate their contents: protein degradation (in Amélassiwa, Ketcheyi, and Siéloune) to release proline for osmotic adjustment or osmoprotection and, conversely, proline mobilization (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), or antioxidant system enzymes such as CAT, APX, POD, etc. (Ramalho et al., 2018; Bokobana et al., 2019), or aquaporins. This issue corroborates the work of Gujjar et al. (2018), who found a negative association between the expression of protein-coding genes (PRPs) and proline levels in tomatoes during water stress,



suggesting 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 deficit they imposed. Hamidou et al. (2007) also found a significant accumulation of proline with non-significant variation in protein content. Regarding MDA accumulation, the water deficit induced an oxidative stress that led to a significant accumulation of MDA. Ketcheyi-Soukpelo highlighted an effective strategy to maintain membrane integrity through a near-zero value of MDA content fluctuation. Thus, the high accumulation in Amélassiwa is an indicator of susceptibility. The positive and strong correlation between MDA levels and total protein levels indicates that proteins were widely mobilized to target ROS damage. PCA revealed three groups, two of which showed a tendency to deviate from the axes. These are varieties that deviated from the average of the assay. For example, Amélassiwa and Ketcheyi exhibited drought susceptibility due to their DSIs. Regarding the group of intermediate or centered varieties (Ketcheyi-Soukpelo and Malgbong-Bomoine), they indeed showed the highest yields in stressed plants, with low DSIs. The last two components (of the three assessed) revealed a group of three varieties strongly correlated with stress variables: Amelassiwa, Ketcheyi, and TVX. The latter, an improved variety, exhibited 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.

CONCLUSION

Water deficit induced significant declines in all variables except in PR, PROT and PLN. Varieties exhibited globally close responses under water deficit. They also showed significant variations in varietal type effects, except in PR. A negative correlation between proline and protein contents was noted. This may elucidate some attempts to regulate these biochemical variables. Besides, a significant accumulation of MDA in all varieties was recorded except in Ketcheyi, but with a peak in Amélassiwa. Regarding yield's variables, each variety recorded a decline, with Amélassiwa and Ketcheyi recording the largest ones. Even if most variables did not allow any discrimination, NLE and DSI permitted to segregate varieties into drought-tolerant and drought-susceptible groups. Amélassiwa and Ketcheyi exhibiting very high DSIs and losses in NLE are considered as drought-susceptible varieties. With the lowest DSI, Ketcheyi-Soukpelo is the most tolerant variety, thereby a good candidate for a breeding program that includes drought resistance. Cultivation of Amélassiwa and Ketcheyi requires specific irrigation mechanisms well adapted to local agroecological conditions, especially during sudden drought periods. Exploring more local varieties' adaptive mechanisms and identifying new, more productive, and tolerant varieties with additional variables would be a crucial asset for agriculture and breeding programs. In time, farmers will have access to high-performing varieties that yield well under conditions of water scarcity.



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