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Tolerance Traits and Dry Matter Partitioning in Five Maize (*Zea mays* L.) Varieties Subjected to Drought Stress during the Vegetative Phase

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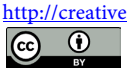


Abstract

Maize (*Zea mays* L.) is particularly vulnerable to drought stress due to its high water requirements. The aim of this study is to assess the tolerance to drought stress induced during the vegetative phase in five maize varieties (Samaz, TZPB, Ikenne, TZE and Amen) and to understand the dry matter partitioning involved. The results showed that flowering (male or female) is only slightly affected, delayed by two days in the Ikenne variety and by three days in the Amen variety, but not affected at all in the Samaz, TZPB, and TZE varieties. Under drought stress, all varieties exhibit a relatively small decrease in relative water content of between 2.5 and 15.5%. Osmoregulation remains more efficient in the Ikenne variety, with a high foliar proline accumulation of around 300%. Oxidative stress is moderate overall, with foliar malondialdehyde accumulation approaching 45% in the Samaz and TZPB varieties. Calculation of the drought susceptibility index (DSI) shows that the Ikenne and TZE varieties are tolerant (DSI < 1), the Samaz and TZPB varieties are sensitive (DSI > 1), and the Amen variety is intermediate (DSI = 1). The TZPB, Samaz, Ikenne and Amen varieties prioritise biomass allocation to root growth (soil exploration) and/or above-ground growth (stems and leaves) at the expense of grain formation (reproduction), whereas the TZE variety prioritises reproduction at the expense of vegetative growth. These results could provide promising avenues for selecting varieties more resilient to increasing drought stress.

Keywords

Climate Change, Drought, Maize, Tolerance

1. Introduction

Maize (*Zea mays* L., 2n = 2× = 20, family Poaceae) is the most important cereal crop after wheat followed by rice in the world and is the first in Sub-Saharan Africa where over 80% of the population depends on it as a source of food, income and livelihood [1]. It is a multidisciplinary crop and used in human food, animal feed, fodder and bioenergy production. In Togo, maize is a staple food in most households and remains the most widely grown cereal crop, far ahead of sorghum, with 804,000 hectares under cultivation in 2024 and a production of around 1,010,000 tonnes [2]. The crop has tremendous potential as one of the main sources of food for the rapidly increasing population. Unfortunately, climate change's sustained temperature rise causes drought stress, which threatens the stability of maize output [3] [4].

For several decades now, Togo has been facing climate change characterised by rising temperatures, reduced rainfall and a shift in the rainy season, phenomena frequently observed particularly in the southern part of the country [5]-[7]. An analysis of meteorological data for the period 1961-2018 clearly reveals a certain shift in the country's climate, characterised by marked spatial and temporal variability. Temperatures are generally on the rise, with an increase of between 0.8˚C and 1.2˚C across the country's latitudes [8]. Rainfall is generally decreasing across the whole country, with a reduction ranging from 15 mm to 98 mm of rain. This climate trend gives rise to climate-related risks, including floods, droughts, heatwaves, shifts in the seasons, strong winds, uneven rainfall distribution and coastal erosion, with far-reaching consequences for ecosystems and livelihoods [9]. Furthermore, there has been a decline in the precipitation-to-potential evapotranspiration (P/ETP) ratio, reflecting the trend towards a drier climate [10].

This deterioration in rainfall and temperature patterns makes Togolese agriculture extremely vulnerable. Farming schedules are disrupted by an increasingly unpredictable climate [5], leading to soil erosion and sometimes destroying crops, with significant negative repercussions on yields [11]. In some regions, crops such as maize wither before they have even reached maturity. Sometimes, less than 60% of the water requirements during maize flowering are met, to the extent that yields become very low, regardless of water conditions during the rest of the growing season [12]. In the south of the country, the premature end to the rainy season is reducing the chances of maize producing ears; and even if it does, the ears are empty of seeds inside their husks. However, the rural population is predominantly poor and relies mainly on the exploitation of natural resources and rain-fed agriculture, which is severely affected by climatic phenomena. Consequently, in order to survive, farmers are turning away from agriculture in favour of small-scale trade in imported manufactured goods, or are simply leaving the countryside altogether. Land previously used for food crops is gradually being replaced by small brickworks and eucalyptus plantations [5] [13].

A major barrier to the production of maize is drought stress, which occurs when there is a lack of water. This results in decreased yield components, leaf photosyn-

thesis, and transpiration in maize plants [14]. Although there are several environmental factors that can affect maize productivity, drought is thought to be the most significant one affecting the production of maize [15]. The most vulnerable stages of maize to drought stress are the silking, vegetative, and ear stages, which could result in yield decreases of up to 25%, 50%, and 21%, respectively [16]. Drought during the flowering stage has a significant impact on both kernel set and grain filling since the crop is so susceptible to it [17]. Drought stress affects growth rates during the vegetative stage of maize by lowering the active photosynthetic leaf area of the crop canopy; this causes a loss in yield at maturity because it extends the anthesis-silking interval and limits grain weight [18].

Global climate change will result in an increase in the frequency of drought disasters [19], which will cause major swings in maize yield and ultimately uncertain food security [20]. In light of this situation, adapting agriculture involves, on the one hand, identifying and adopting varieties capable of withstanding the new climatic conditions and, on the other hand, identifying susceptible varieties in order to implement breeding or resilience programmes. It is therefore necessary to have drought-resistant varieties with high yield potential in order to maintain productivity and ensure food security [21]. This study was conducted with this in mind; it aims to assess the physiological, biochemical and yield-related responses of the five most widely grown maize varieties in Togo to induced water stress.

2. Materials and Methods

2.1. Plant Material and Trial Conduct

The plant material used consists of seeds from five maize genotypes sourced from the gene bank of the Togolese Institute of Agricultural Research. These varieties are Ikenne, TZE, Amen, Sammaz 52, and TZPB, whose agromorphological characteristics are presented in **Table 1**. The experiment was conducted in a greenhouse at the Littoral Agricultural Research Center, Davié, Togo (6˚10' N and 1˚12' E), between May and August 2025. The seedlings are grown in 17-liter plastic pots (31 cm tall, with a diameter of 31 cm at the top and 21 cm at the bottom) that have holes in the bottom to allow water to drain after watering. The pots were placed on curved plastic trays to collect excess water and prevent the roots from growing through and into the soil. The experimental design is a split-plot arrangement organized into 3 blocks with two interacting factors: cultivar and irrigation regime. The experimental unit consists of 3 pots for each treatment (control, stress), for a total of 90 pots across the five genotypes (**Figure 1**). Each pot is filled with 20 kg of substrate consisting of soil collected from the root zone (0 - 25 cm) of the experimental site, sieved (2 mm), heat-sterilized (60 - 65˚C), and mixed with 1.5 g of 15-15-15 NPK fertilizer and 0.75 g of urea. The physicochemical characteristics of the culture medium are presented in **Table 2**. The soil available water capacity (AWC) of the culture medium was calculated using the equation proposed by Baize [22]:

$$AWC = \left(\theta fc - \theta wp\right) \times D$$

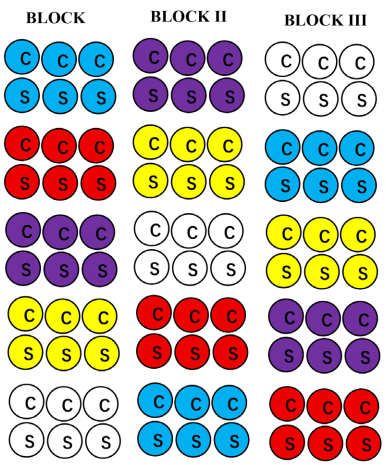
AWC: soil available water (mm); θfc: volumetric water content at field capacity

(mm/m), θwp: volumetric water content at permanent wilting point (mm/m); D: soil depth in the pot (m).

Table 1. Agronomic characteristics of the corn varieties studied.

Corn varieties	Genetic nature	Breeder and year of creation	Growing cycle from sowing to 50% maturity (days)	Plant height (cm)	Grain color	1000-grain weight (g)	Grain texture	Potential yield (t/ha)	Other characters
Samaz (Sammaz 52)	Synthetic	IITA (2017)	110 - 120	190 - 195	Orange	260	Flint corn	6	Moderate content of provitamin A
TZPB (TZPB SR W Bénin)	Synthetic	IITA (1978) INRAB (1990)	115 - 120	220	White	320	Flint corn	6	Good lodging resistance, moderate resistance to Striga
Ikenne (Ikenne 9449 SR)	Composite	IITA (1980)	100 - 105	190 - 210	White	300 - 330	Dent corn	5	Good lodging resistance, resistant to corn leaf streak
TZE (TZEE W Pop STR QPM)	Composite	IITA (2000)	80 - 85	170 - 185	White	230 - 250	Semi-dent corn	4	Good lodging resistance, resistance to Striga, resistant to corn leaf streak, rich in lysine and tryptophan
Amen	Synthetic	INCV/ITRA (1992)	90 - 100	200 - 210	White	200 - 300	Semi-dent corn	4	Lodging resistance, resistance to Striga, resistant to corn leaf streak,

Source: CNSP [24].



Calculation of the soil available water capacity (AWC)

Soil texture : Sandy loam
θfc = 265 mm
θwp = 104 mm
$\theta fc - \theta wp$= 161 mm
Soil depth in the pot = 0.272 m
AWC = 43.792 mm
30% AWC = 13.1376 mm
70% AWC = 30.6544 mm

Water volumes

1 mm = 1 $L.m^{-2}$
Top surface of the pot at substrate level = 0.08 m^2
$V_{(30\% AWC)}$ = 1.056 L
$V_{(70\% AWC)}$ = 2.46 L

Moisture content (MC)

$$MC_{(30\% AWC)} = \frac{1.056\ Kg}{20\ Kg} \times 100 = 5.28\%$$

$$MC_{(70\% AWC)} = \frac{2.46\ Kg}{20\ Kg} \times 100 = 12.3\%$$

C: control; S: Drought stress.

Figure 1. Experimental device (Split Plot 2 × 3). The different colors represent the different varieties.

Table 2. Physicochemical characteristics of the culture substrate (before adding NPK and urea).

Parameters	Content
Total organic matter	1.3%
Total organic carbon	0.750%
Total nitrogen	0.0482%
Assimilable phosphorus	6.860 mg/kg
Exchangeable calcium	5.231 meq/100g
Exchangeable magnesium	0.972 meq/100g
Exchangeable potassium	0.189 meq/100g
pH-H_2O (1/2.5)	6.345
Electrical conductivity (1/5)	20.20 µS/cm
Clay	9%
Silt	28.5%
Sand	62.5%
Field capacity (mm/m)	265
Permanent wilting point (mm/m)	104

A pre-planting irrigation was applied every 2 days at the field capacity, until the sowing on the 15th day (May 28, 2025). Maize seeds, after being kept wet in the darkness for 72 hours, were planted in pots (04 seeds/pot). After germination, irrigation was reduced to 70% of the AWC. The separation which was achieved on the 14th day after sowing allowed to maintain one plant by pot. Drought stress was induced on July 2, 2025 (35 days after sowing), midway through the vegetative phase for the Ikenne, Samaz, and TZPB varieties (medium- to long-cycle varieties) and at the end of the vegetative phase for the TZE and Amen varieties (short-cycle varieties). This period naturally coincides with the scarcity of rainfall in southern Togo, marking the end of the main rainy season (March through July) and the beginning of the short dry season (August through September). It perfectly simulates rain-fed corn cultivation, which typically completes its growing cycle during a period of water scarcity, especially when planting is delayed (in May) due to a lack of potentially beneficial rainfall. The applied drought stress was about a lowering of the irrigation from 70% of the AWC (control) to 30%. The water content of the pots was adjusted daily after the moisture was measured using a probe-type hygrometer.

The water deficit period lasted 14 days, which corresponds to the average duration of drought episodes recorded during the growing seasons in southern Togo [23]. At the end of this period, the height of the plants (from the base of the stem to its tip) was measured using a tape measure, and samples of fresh leaves were collected between 8:00 and 9:00 a.m. from the youngest, fully developed leaf. The

leaf samples collected were immediately wrapped in aluminum foil and stored at −4˚C until biochemical analyses were performed one week later. Then, irrigation of the stressed plants was resumed as for the control plants, that is, at 70% of the SAW. Manual pollination was also performed during this period. To do this, the ears were first covered with a protective sleeve before the stigmas appeared. Once the stigmas appeared, pollen was collected from one plant and then manually applied to another plant of the same variety that had undergone the same treatment. The dates of male and female flowering were recorded for each pot. The environmental conditions in the greenhouse during the trial period were as follows: a 12-hour photoperiod, average temperatures of 26.4˚C/29.6˚C/26.8˚C at 8 a.m./2 p.m./5 p.m., and relative humidity of 90.8%/87.1%/94.2%.

2.2. Relative Water Content (RWC)

The RWC content was calculated using the standard formula [(FW − DW)/(HydW − DW) * 100] previously determined by Farrant [25], where FW, HydW and DW are the leaf fresh weight, hydrated (full turgor) and dry weights, respectively. The hydrated weight was determined by weighing the leaf after 24 h of immersion in distilled water in a sealed flask at room temperature. Dry weight was determined gravimetrically after 48 h at 70˚C in an oven.

2.3. Total Protein Content

Fresh leaf tissues (0.5 g) were powdered in a cold mortar with liquid nitrogen and homogenised in 2 mL of 50 mM sodium phosphate buffer (pH 7.0) containing 1 mM ethylenediamine tetraacetic acid (EDTA), 1 mM ascorbic acid and 2% (w/v) polyvinylpyrrolidone (PVP). The homogenate was centrifuged at 4˚C/12 000 rpm for 10 minutes. The resulting supernatant was used for the assay of total protein by the method of Bradford [26] using a standard curve established with bovine serum albumin (BSA). The protein content was expressed as mg of protein per g of fresh weight.

2.4. Proline Content

The proline content was determined using the method of Bates *et al.* [27]. 250 mg of fresh plant leaf was powdered in a cold mortar with liquid nitrogen and homogenised in 5 mL of sulphosalicylic acid 3% (w/v). The homogenate was filtered through a n˚ 2 filter paper (Whatman® n˚ 2). 2 mL of the filtrated sample was mixed with 2 mL of glacial acetic acid and 2 mL of freshly prepared acid-ninhydrin reagent [warming 1.25 g ninhydrin in 30 mL glacial acetic acid, and adding 20 mL phosphoric acid 6 M] in test tubes. After agitation, the sample was incubated at 100˚C for 1 hour, and this produces the coloured complex formation. The reaction was finally stopped in ice followed by the addition of 4 mL toluene and vortexing for 15 - 20 s. The organic phase containing the chromophore was collected, and absorbance at 520 nm was measured spectrophotometrically. The proline content was determined as µmol of proline per g of fresh

weight using a standard curve.

2.5. Malondialdehyde (MDA) Content

MDA content was measured following the method of Heath and Packer [28]. 500 mg of fresh plant leaf was powdered in a cold mortar with liquid nitrogen and homogenised in 10 mL 0.1% (w/v) trichloroacetic acid (TCA). The homogenate was centrifuged at 10.000 g for 10 min. To 1 mL aliquot of supernatant, 4 mL 0.5% (w/v) thiobarbituric acid (TBA) in 20% (w/v) TCA was added. The mixture was heated at 95˚C for 30 min and then quickly cooled in an ice bath. After centrifugation at 10,000 g for 10 min, the absorbance of the supernatant was recorded at 532 nm. The value for nonspecific absorption at 600 nm was subtracted. MDA content was expressed as µmol MDA per g of fresh weight using an extinction coefficient of 155 mM^{-1} cm^{-1}.

2.6. Measurement of Biomass and Grain Yield Components

At harvest time, the plants are pulled up and then cut at the base of the stem. Soil particles are removed from the root system by washing in a fine-mesh sieve to preserve all root biomass. The above-ground dry weight (ADW) and the root dry weight (RDW) were obtained after drying in an oven at 70˚C for three days. The harvested grains are also oven-dried at 70˚C for three days, then weighed. The following yield components are then measured: grain dry weight per plant (GDWP), number of grains per plant (NGP), 100-grain weight (100 GW), and individual grain weight (IGW). By substituting yield with DGWP, which is its main component, the drought sensitivity index (DSI) for each variety studied was calculated using the formula developed by Fischer and Maurer [29]. A variety is considered tolerant if the calculated DSI is less than 1, or sensitive if the calculated DSI is greater than 1.

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

DSI: Drought Sensitivity Index; *R*: RcS/RcT, where RcS corresponds to the variety's yield under drought stress and RcT to the variety's yield under optimal irrigation; *D*: drought intensity, $D = 1 - (RMS/RMT)$, where RMS corresponds to the average yield of all varieties under drought stress and RMT to the average yield of all varieties under optimal irrigation.

2.7. Statistical Analysis

All data presented represent the averages of the 9 replicates from all three blocks of the experiment. The data were analyzed using the R software (version 4.5.2). Analyses of variance (ANOVA) were used to determine whether the measured parameters showed significant differences between water conditions for the different varieties. The interpretation of the results was based on the p-values from the ANOVAs, with a significance level set at 0.05. Two classification factors were used: the standard factor for variety type and the water regime. Principal compo-

nent analysis combined with a biplot was used to distinguish the different maize varieties based on their adaptive responses to water stress.

3. Results

The analysis of variance shows that the irrigation regime, the cultivar, and the interaction between these two factors had a highly significant effect ($p = 0.001$ to $p < 0.05$) on the measured variables. However, specific patterns were observed in the variations in the measurements from one cultivar to another and depending on the irrigation regime applied.

3.1. Physiological and Biochemical Responses

Drought stress had no significant effect on the dates of male flowering (appearance of the panicle) and female flowering (appearance of silks) in the Samaz, TZPB, and TZE varieties (Table 3). In contrast, it delayed these dates by two days in the Ikenne variety and by three days in the Amen variety. Furthermore, the difference between male and female flowering did not change significantly under drought stress, regardless of the variety. In addition, drought stress caused a significant growth retardation in the Samaz, TZPB, and Ikenne varieties, by 20%, 26.29%, and 16%, respectively, compared to their controls (Table 4). All corn varieties maintained their water status under drought stress within a very narrow range, with a decrease in RWC of less than 16% compared to the control. The Amen variety was the one whose water status was most affected by water stress. All maize varieties accumulate proline at the expense of total protein content under drought stress. The Ikenne variety stands out in particular for having the highest proline accumulation and the greatest decrease in total protein content, representing an increase of 297.22% and a decrease of 49.46%, respectively, compared to the control. Oxidative stress induced by water stress is characterized by a moderate accumulation of MDA, with the Samaz and TZPB varieties being the most affected, exhibiting the highest MDA accumulation rates—44.76% and 43.09%, respectively—compared to their controls.

3.2. Biomass and Grain Yield Responses

Drought stress resulted in a significant decrease ($p < 0.05$) in above-ground dry weight (ADW) in the TZE and Amen varieties, by 45.99% and 30.88%, respectively, compared to their controls, while a non-significant decrease was observed in the Samaz variety and a non-significant increase in the TZPB and Ikenne varieties (Table 5). Root dry weight (RDW) was also strongly influenced by drought stress, with a negative effect observed in the Samaz variety—a significant decrease of 36.76% compared to the control—and a positive effect observed in the TZPB variety—an increase of 108.69% compared to the control. In contrast, this parameter was not significantly affected by water stress in the Amen, TZE, and Ikenne varieties, although downward and upward trends were observed, respectively. These differences in the impact of water stress on above-ground dry weight, root dry weight, and grain dry weight imply different strategies for allocating biomass

(photoassimilates) to the various organs (Figure 2).

Table 3. Effect of drought stress on flowering.

Variety	Treatment	Male flowering date (Days after sowing)	Female flowering date (Days after sowing)	Difference between male and female flowering (Days)
Samaz	Control	52.25 ± 2.52[a]	53.36 ± 2.45[a]	1.23 ± 0.11[a]
	Drought	52.37 ± 2.13[a]	53.10 ± 2.38[a]	1.37 ± 0.09[a]
TZPB	Control	53.57 ± 1.18[a]	55.41 ± 1.24[a]	2.41 ± 0.17[a]
	Drought	53.34 ± 0.99[a]	55.13 ± 1.66[a]	2.59 ± 0.2[a]
Ikenne	Control	48.42 ± 2.03[b]	50. 28 ± 2.21[b]	2.18 ± 0.12[a]
	Drought	52.23 ± 1.97[a]	54.59 ± 2.41[a]	2.36 ± 0.16[a]
TZE	Control	48.13 ± 2.73[a]	50.14 ± 1.89[a]	2.22 ± 0.10[a]
	Drought	48.25 ± 2.34[a]	50.48 ± 2.01[a]	2.65 ± 0.14[a]
Amen	Control	48.31 ± 1.98[b]	51.33 ± 2.42[b]	3.24 ± 0.59[a]
	Drought	51.56 ± 2.07[a]	54.61 ± 2.11[a]	3. 88 ± 0.30[a]

Different letters in each row mean statistically different ($p < 0.05$) based on Tukey test.

Table 4. Effect of drought stress on growth and biochemical parameters.

Variety	Treatment	Plant height (cm)	Relative water content (%)	Total protein (mg/g FW)	Proline (mg/g FW)	Malondialdehyde (μmol/g FW)
Samaz	Control	116.67 ±7.64[a]	72.22 ± 7.70[a]	22.15 ± 3.08[a]	0.99 ± 0.01[b]	51.40 ± 4.34[b]
	Drought	93.33 ± 6.89[b]	68.91 ±6.07[b]	15.72 ± 3.79[b]	1.2 ± 0.05[a]	74.41 ± 3.80[a]
TZPB	Control	136.00 ± 5.77[a]	66.57 ± 4.80[a]	30.73 ± 3.09[a]	0.91 ± 0.06[b]	40.43 ± 2.62[b]
	Drought	100.24 ± 6.00[b]	61.67 ± 4.69[b]	25.87 ± 3.17[b]	1.09 ± 0.07[a]	57.85 ± 3.14[a]
Ikenne	Control	127.00 ± 6.15[a]	67.42 ± 2.66[a]	26.81 ± 1.83[a]	0.36 ± 0.03[b]	44.52 ± 2.65[b]
	Drought	106.67 ± 6.58[b]	65.74 ± 3.85[a]	13.55 ± 1.36[b]	1.43 ± 0.08[a]	54.41 ± 2.72[a]
TZE	Control	109.00 ± 5.22[a]	57.32 ± 5.86[a]	26.39 ± 1.29[a]	0.62 ± 0.05[b]	52.47 ± 2.85[b]
	Drought	107.33 ± 5.58[a]	51.93 ± 6.44[b]	17.58 ± 2.94[b]	1.11 ± 0.05[a]	63.87 ± 2.53[a]
Amen	Control	132.67 ± 6.64[a]	66.75 ± 5.93[a]	24.58 ± 2.09[a]	0.95 ± 0.02[b]	50.54 ± 2.45[b]
	Drought	129.22 ± 6.52[a]	56.44 ± 1.71[b]	15.43 ± 1.78[b]	1.83 ± 0.08[a]	58.77 ± 2.55[a]

Different letters in each row mean statistically different ($p < 0.05$) based on Tukey test.

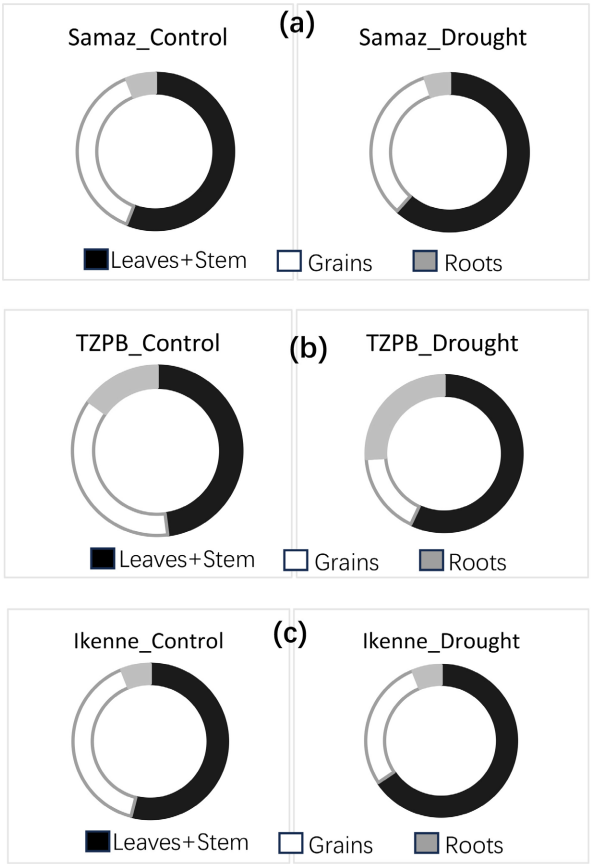
Table 5. Effect of drought stress on biomass and major yield parameters.

Variety	Treatment	Above-ground dry weight ($g \cdot plant^{-1}$)	Grain dry weight per plant ($g \cdot plant^{-1}$)	Root dry weight ($g \cdot plant^{-1}$)	Total dry weight ($g \cdot plant^{-1}$)	100-grain weight (g)	Individual grain weight (mg)	Number of grains per plant	Drought sensitivity index
Samaz	Control	137.70 ± 34.19[a]	90.05 ± 2.29[a]	14.31 ± 1.61[a]	242.06 ± 33.48[a]	22.01 ± 3.26[a]	224.19 ± 25.35[a]	401.33 ± 27.02[a]	1.32

Continued

TZPB	Drought	104.40 ± 27.17^{a}	56.29 ± 4.49^{b}	9.05 ± 1.91^{b}	169.74 ± 31.18^{b}	21.80 ± 2.40^{a}	211.91 ± 17.25^{a}	267.67 ± 36.56^{b}	1.64
	Control	127.47 ± 24.50^{a}	97.25 ± 4.13^{a}	38.31 ± 6.06^{b}	263.02 ± 26.42^{a}	30.94 ± 4.15^{a}	304.50 ± 19.29^{a}	315.00 ± 29.14^{a}	
Ikenne	Drought	175.27 ± 21.33^{a}	52.33 ± 7.11^{b}	79.95 ± 5.14^{a}	307.55 ± 38.51^{a}	28.20 ± 1.89^{a}	282.99 ± 25.65^{a}	182.33 ± 19.66^{b}	0.71
	Control	110.07 ± 19.93^{a}	78.95 ± 5.52^{a}	13.35 ± 1.63^{a}	202.37 ± 56.56^{a}	32.11 ± 2.41^{a}	320.93 ± 10.21^{a}	244,33 ± 49,86^{a}	
TZE	Drought	145.40 ± 27.83^{a}	62.92 ± 4.9^{a}	13.65 ± 1.33^{a}	221.96 ± 36.46^{a}	29.91 ± 4.12^{a}	281.33 ± 10.54^{a}	222.00 ± 15.72^{b}	0.25
	Control	171.13 ± 23.76^{a}	85.3 ± 6.21^{a}	15.59 ± 3.76^{a}	272.02 ± 23.76^{a}	27.74 ± 5.49^{a}	271.89 ± 13.88^{a}	312.67 ± 47.75^{a}	
Amen	Drought	92.43 ± 15.88^{b}	79.65 ± 4.6^{a}	10.41 ± 2.3^{a}	182.49 ± 28.65^{b}	25.06 ± 3.20^{a}	256.74 ± 27.05^{a}	310.67 ± 22.94^{a}	1
	Control	131.27 ± 13.57^{a}	85.76 ± 5.98^{a}	13.38 ± 2.56^{a}	230.41 ± 15.75^{a}	26.41 ± 2.56^{a}	251.73 ± 17.48^{a}	340.00 ± 18.25^{a}	
	Drought	90.73 ± 8.01^{b}	61.51 ± 5.80^{b}	13.12 ± 1.44^{a}	165.37 ± 14.15^{b}	23.19 ± 2.87^{a}	222.85 ± 18.74^{a}	276.67 ± 50.3^{b}	

Different letters in each row mean statistically different ($p < 0.05$) based on Tukey test.



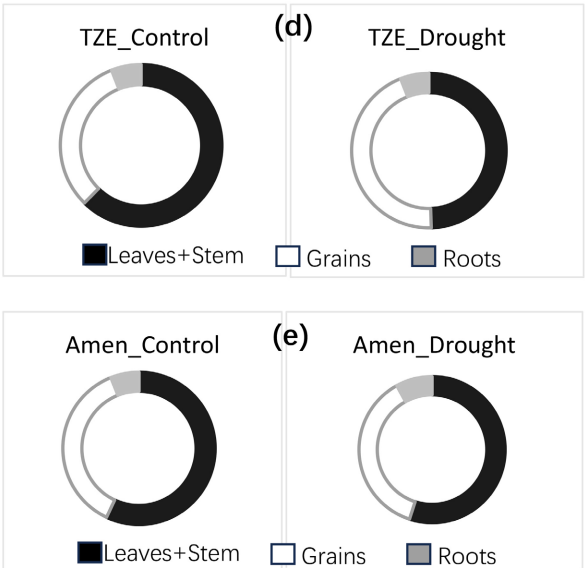


Figure 2. Strategies for allocating biomass among different organs under induced drought stress.

Drought stress resulted in a significant decrease ($p < 0.05$) in grain yield—represented here by grain dry weight per plant (GDWP)—in the Samaz, TZPB, and Amen varieties, with respective decreases of 37.49%, 46.19%, and 28.27% compared to their controls (**Table 5**). This decrease was not significant in the TZE and Ikenne varieties. Under these conditions, the number of grains per plant (NGP) remains the only major yield component to have been significantly affected ($p < 0.05$), although a non-significant decrease was observed for individual grain weight (IGW) and 100-grain weight (100 GW) in all varieties. Thus, a decrease in NGP of 33.30%, 42.11%, 9.14%, 0.63%, and 18.63% was observed, respectively, in the Samaz, TZPB, Ikenne, TZE, and Amen varieties compared to their controls. The drought sensitivity index (DSI) calculated for each maize variety shows that the Ikenne and TZE varieties are drought-tolerant ($DSI < 1$), that the Samaz and TZPB varieties are drought-sensitive ($DSI > 1$), and that the Amen variety falls between the two ($DSI = 1$).

3.3. Dry Matter Partitioning in Response to Drought Stress

The interpretation of the distribution of dry matter among the different organs (stem + leaves, roots, and grains) in response to drought stress is based on the variation in the percentage of an organ's dry mass relative to the total dry mass between the control and the stress treatment. Thus, a strategy is considered "priority" when this percentage for the representative organ is higher in the stress treatment than in the control. Thus, when soil moisture becomes scarce, the Samaz variety allocates a significant portion of its biomass to the aboveground parts (stalk and leaves) at the expense of the kernels and roots (**Figure 2(a)**); maintaining the structural integrity of the stalk and leaves therefore remains the plant's priority, which is thus threatened. Under the same unfavorable water conditions, the TZPB variety concentrates

its biomass in the aboveground parts (stems and leaves) and, above all, in the roots, at the expense of the grains (Figure 2(b)); soil exploration remains the priority. In addition, the Ikenne variety shifts biomass allocation from the grains to the aboveground parts (stems and leaves), while keeping it constant in the roots (Figure 2(c)). The TZE variety employs a unique strategy for biomass allocation under drought stress. Under these conditions, the proportion of biomass allocated to grains increases at the expense of the aboveground parts (stems and leaves) (Figure 2(d)). The proportion of biomass allocated to roots remains unchanged compared to the control. In this case, reproduction remains the priority. In the Amen variety, the distribution of biomass among the different parts of the plant does not appear to vary significantly under drought stress compared to the control; however, to a lesser extent, the proportion of biomass allocated to the roots increases at the expense of the aboveground parts (stem and leaves) (Figure 2(e)).

3.4. Principal Component Analysis (PCA) of Parameters under Drought Stress

The PCA biplot (Figure 3) shows the clustering of maize varieties based on the trends of the various variables measured under drought stress. The PC1 and PC2 components explain 48.2% and 27.5% of the total variance, respectively. All measured parameters contribute significantly to the assessment of the effect of water stress on the crop, with the exception of 100 GW, IGW and RWC. The variables evolve in the same way within the total dry weight (TDW), RDW, and ADW vector groups on the one hand, and the NGP, GDWP and plant height vector

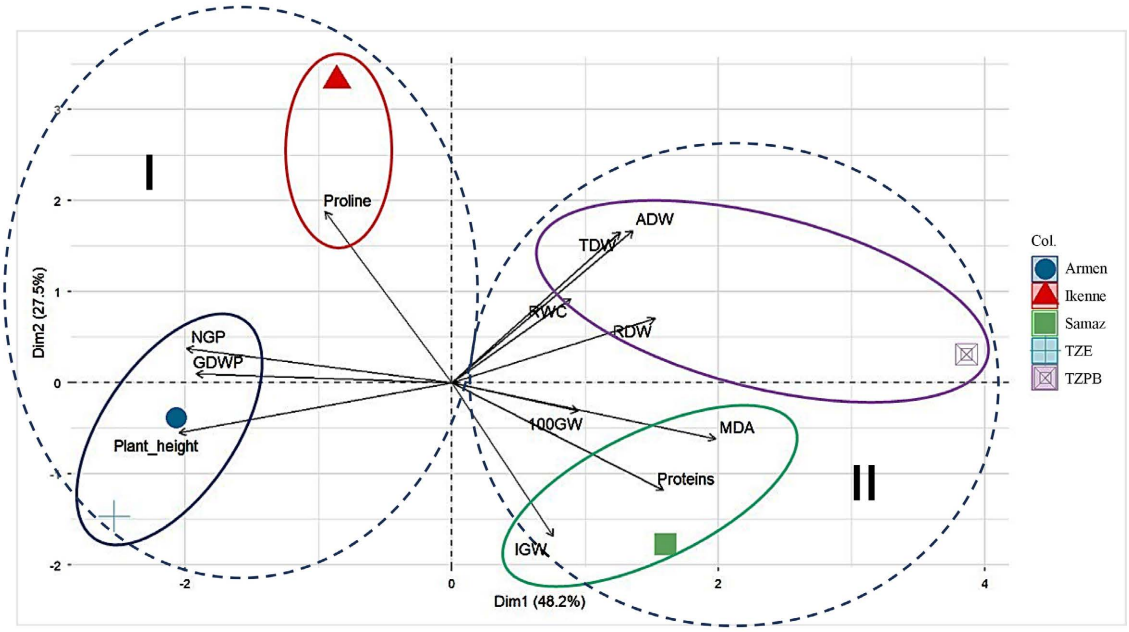


Figure 3. Biplot of the PCA for the measured parameters and maize varieties subjected to drought stress. RWC: relative water content, MDA: malondialdehyde, ADW: above-ground dry weight, RDW: root dry weight, GDWP: grain dry weight per plant, TDW: total dry weight, NGP: number of grains per plant, 100 GW: 100-grain weight, IGW: individual grain weight.

groups on the other, such that an increase (or decrease) in one is accompanied by an increase (or decrease) in the other. However, these two groups of vectors move in opposite directions, reflecting the different resource allocation strategies for the various organs mentioned earlier. The Proline vector moves in the opposite direction to the Protein and MDA vectors, such that an increase in the former leads to a decrease in the latter two (and vice versa), highlighting opposing dynamics among these groups of parameters under drought stress conditions.

Two major groups of varieties appear to emerge, within which various adaptive responses to drought stress are observed:

- The first group (I) includes the varieties TZE, Ikenne, and Amen: these are varieties that were less affected by drought stress in terms of yield. The variables defining grain yield—namely GDWP and NGP—are associated with the TZE and Amen varieties. The drought stress tolerance variable, proline, which characterizes the efficiency of osmoregulation under drought stress, is associated with the Ikenne variety.
- The second group (II) includes the TZPB and Samaz varieties: these are varieties whose yield was significantly affected by water stress. The TZPB variety clearly diverges from the variables that define grain yield (GDWP, NGP), but aligns with the variables that define vegetative growth, notably RDW, ADW, and TDW; it also aligns with the water stress sensitivity variable, notably MDA, which characterizes oxidative stress. The Samaz variety, for its part, aligns with the Protein variable, which characterizes the enzymatic metabolism associated with drought stress.

4. Discussion

An analysis of the physiological and biochemical responses of different maize varieties to drought stress reveals various mechanisms that enable them to adapt to this situation, including slowed growth, maintenance of the plant's water status, proline accumulation, suppression of lipid peroxidation, and the reallocation of resources to different organs.

4.1. Growth Retardation and Low Water Loss in Maize Plants under Drought Stress

Drought stress caused significant growth retardation in the Samaz, TZPB, and Ikenne varieties, which are long-season maize varieties. Welcker *et al.* [30] and Gomaa *et al.* [31] obtained similar results in maize in response to prolonged moderate or severe drought stress induced during the vegetative phase. In this case, growth retardation is generally attributed to a decrease in cell turgor, which limits cell elongation and division in areas of active growth, as well as to the mobilization of resources to implement strategies for adapting to the induced stress [32] [33]. However, the TZE and Amen varieties, which are short-season varieties, were not significantly affected by water stress, although a downward trend was observed. This result can be partly explained by the fact that drought stress occurred toward

the end of the vegetative phase for these varieties. On the other hand, this can also be explained by the low water loss observed in corn plants (TRE < 15%). Indeed, under drought stress, maize exhibits isohydric behavior, meaning that it effectively regulates stomatal opening during periods of water scarcity while maintaining leaf water potential within a narrow range [34] [35]. Under these conditions, the plant continues to produce dry matter and regulates its temperature more effectively, but it consumes more of the water available in the soil. This proves beneficial when rainfall resumes or irrigation is implemented, as was the case in our study, but it is no longer beneficial if the water deficit persists, as the plant will then deplete its water reserves more quickly. Thus, the plant's response to water stress depends not only on its intensity (moderate or severe) but also on its duration.

4.2. Accumulation of Proline and MDA under Drought Stress

The accumulation of proline observed under drought stress is one of the most important mechanisms in plants for mitigating the effects of salt and water stress. It contributes to the regulation of cellular osmotic balance, thereby enabling plant cells to maintain their turgor and metabolism under drought stress [36]. Proline is a key osmoprotectant that stabilizes protein and membrane structures as well as the photosynthetic apparatus [37] [38]. Plants that accumulate higher levels of proline exhibit greater stress tolerance [39] [40], which promotes their growth by reducing nutritional imbalances, decreasing element toxicity, and improving photosynthesis [41] [42]. Furthermore, proline enhances antioxidant activity, thereby reducing oxidative damage [43] [44]. Several studies have confirmed this adaptive role of proline in maize. Ayub *et al.* [45] observed an accumulation of proline in maize grown under drought stress. Ali *et al.* [37] and Khan *et al.* [46] demonstrated that exogenous proline supplementation improves drought tolerance and growth in maize grown under drought stress. Bokobana *et al.* [47] observed a significant accumulation of proline in maize grown under drought stress, particularly when the soil was amended with compost. The accumulation of proline may result from three complementary processes: stimulation of its biosynthesis, inhibition of its oxidation, and/or protein denaturation.

Malondialdehyde (MDA), the end product of ROS-induced lipid peroxidation, increased in all the maize varieties studied, indicating genuine oxidative stress. However, this increase was less pronounced in the varieties with the highest proline contents (Ikenne, TZE and Amen). This reflects greater tolerance to water deficit and better membrane stability in these varieties. These observations corroborate those of Parveen *et al.* [48], who showed that water deficit-induced proline accumulation and the activation of the antioxidant defence system were negatively correlated with lipid peroxidation.

Although some studies have shown that drought stress leads to an increase in total protein content in maize leaves compared to controls [49], our results, on the contrary, reveal a decrease in these metabolites. This contrasting result appears to depend heavily on the genotypes studied, the timing of drought stress induc-

tion, its duration, and/or its intensity [45]. Indeed, severe or prolonged drought stress (as was the case in our study) could potentially overwhelm the plants' adaptive mechanisms [49]. Consequently, we observe degradation of structural proteins (such as parietal proteins) and inhibition of the synthesis mechanisms of specific stress-associated proteins, such as LEA (Late Embryoge nesis Abundant) proteins, heat shock proteins (HSPs), and enzymes of the antioxidant system.

4.3. Changes in the Dry Weight of Different Plant Parts and Grain Yield in Response to Drought Stress

The study showed that maize exhibits a greater reduction in total dry weight under drought stress in the Samaz, TZE and Amen varieties, with losses ranging from 20 to 30 per cent. Similar results have previously been reported for maize by Meskelu *et al.* [50] and Ersel *et al.* [51]. This reduction is thought to be due to a decrease in leaf area and in stem and root elongation [52]-[54], a decrease in the number of grains due to poor fecondation and/or reduced starch accumulation in the grains [55]-[57]. The reduction in above-ground dry weight and root dry weight is an adaptive capacity necessary for the survival of plants exposed to abiotic stress [21] [57] [58]. This enables the plant to accumulate energy and resources to combat stress before the imbalance between the inside and outside of the organism reaches a threshold beyond which the damage becomes irreversible [59]. These losses fall within the low to medium range of decreases reported in the literature, where reductions in dry biomass generally vary between 20% and 55% under conditions of moderate to severe drought [60]. This could be explained by a return to normal irrigation conditions following the stress treatments, suggesting that the restoration of water conditions likely allowed for a partial resumption of vegetative growth, thereby limiting the extent of the losses measured at the end of the cycle. This recovery following the restoration of water conditions is also observed in the literature and depends heavily on the severity and duration of the drought, as well as on the variety [61]. Re-watering can, in particular, help to reduce growth differences between control plants and stressed plants, increase stem diameter [62] and restore leaf length [33]. Unlike the Samaz, TZE and Amen varieties, water stress led to an increase in dry biomass (total, above-ground and root) in the TZPB and Ikenne varieties. This leads us to hypothesise that the reductions in these parameters under drought stress in the Samaz, TZE and Amen varieties are not solely due to reduced growth, but may also reflect strategic reallocations of biomass.

Drought stress had a negative impact on all the yield components assessed in this study. However, the number of grains per plant (NGP) was the component most affected by water stress. Cai *et al.* [62] had also observed that the number of grains per plant remains the yield component most sensitive to water stress. Indeed, grain production is particularly sensitive to water deficit during a period centred on flowering, with maximum sensitivity occurring before male flowering [50]. Any impairment of the vegetative system results, at the floral stage, in a reduction in the number of rows of ovules, followed by a decrease in their length [63]. The plant responds by causing the most fragile—and therefore the young-

est—ovules at the tip of the ear to abort, in order to ensure optimal filling of the remaining grains [64] [65]. The reduction in grain dry weight per plant (GDWP), 100-grain weight (100 GW) and individual grain weight (IGW) observed under drought stress is thought to be linked to reduced availability of carbon assimilates per grain, a consequence of accelerated leaf senescence [66] [67] or a reduction in the transfer of assimilates from the leaves to the seeds (see dry matter reallocation strategies discussed earlier). It could also have been linked to a shorter grain-filling period [68], had the water deficit been applied at the milky grain stage. Indeed, the amount of carbon assimilates available per organ is modulated by the functioning of the photosynthetic organs and by the number of storage sites [63]. Thus, if the water deficit were applied at the male flowering stage, a compensatory phenomenon would occur; in this case, the assimilates would be available to the few viable grains [69].

4.4. Dry Matter Partitioning among Different Plant Organs in Response to Drought Stress

Under drought stress, the adjustment of dry matter distribution among the plant's various organs is recognised as an important adaptive strategy that enables the plant to prioritise certain vital functions [62] [70]. Plants often reduce growth in the above-ground parts to limit transpiration whilst favouring root allocation in order to improve water uptake [71]. In parallel with root allocation, a slight increase in the proportion of leaves is observed [72]. Conversely, the proportion of biomass allocated to reproductive organs (ears, silks, husks) is reduced, which may compromise grain yield. The proportion of biomass allocated to supporting structures, such as stems, is also reduced [72]. The redistribution of biomass towards vegetative parts, at the expense of reproductive parts in the Samaz, Ikenne, TZPB and Amen varieties, also appears to reflect a better recovery of vegetative functions following rehydration. Furthermore, improved water extraction from the soil is only effective if the soil contains water. Thus, the TZPB and Amen varieties would have a significant advantage in soils with very good available water reserves or in the event of a rapid return of rainfall following a drought. However, in less well-supplied conditions, they would consume the available water too quickly, with the disadvantage of causing sudden interruptions in water uptake in soils that are depleted too rapidly. Furthermore, the accumulation of a greater quantity of dry matter in the roots can result in an energy cost that is detrimental to the above-ground parts and grain yield. The Samaz and Ikenne varieties prioritise the allocation of biomass to above-ground growth (stems and leaves) at the expense of reproduction (grains) when subjected to stress. The priority would then be to maintain the structural integrity of the above-ground vegetative tissue, which is key to successful reproduction, particularly as this is a long-cycle variety. This strategy remains beneficial in the short term, but proves fatal when water stress persists over time. Unlike other varieties, the TZE variety prioritises reproduction at the expense of vegetative growth to ensure the survival of the species. However, these

changes are not always significant from one variety to another and must therefore be interpreted with caution

5. Conclusion

This study assessed the adaptive responses of five maize varieties grown in Togo (Samaz, TZPB, Ikenne, TZE, Amen) to controlled drought stress. The results reveal a variety of physiological and biochemical strategies employed by these varieties to mitigate the effects of water stress. From a physiological standpoint, flowering (male or female) was only slightly affected (Ikenne and Amen varieties) or was not affected at all (Samaz, TZPB, and TZE varieties). The five maize varieties studied showed very little variation in relative leaf water content, indicating effective and pronounced stomatal regulation. From a biochemical standpoint, the TZE and Ikenne varieties stood out for their superior integrated tolerance, combining high accumulations of proline with low accumulations of malondialdehyde. In contrast, the Samaz and TZPB varieties recorded low proline accumulation and high malondialdehyde accumulation, characteristic of a low level of tolerance or increased sensitivity. The Amen variety showed moderate tolerance to drought stress, although it accumulated less MDA than all other corn varieties and nearly the same level of proline as the TZE variety. In response to drought, the TZE variety prioritises reproduction at the expense of vegetative growth, whilst the TZPB, Samaz, Ikenne and Amen varieties adopt a resource allocation strategy favouring vegetative growth (above-ground and/or root). These results could provide promising avenues for the selection and improvement of varieties that are more resilient to increasing drought stress.

Author Contributions

Bokobana Atalaèsso: contributed to the study design, laboratory experiments, data analysis, results interpretation and original manuscript writing. Akakpo Etienne M., Mayaba Tawelsi, Ledi Kwassi Kporliawornou and Bodjona Tchaou B. P. I.: contributed to laboratory experiments, data analysis, results interpretation and reviewing and editing original manuscript. Tozo Koffi and Odah Komi: validated and supervised the study and contributed to reviewing and editing original manuscript.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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