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Research Article

Climate-Induced Changes in Functional Traits, Soil Hydraulic Properties, and Drought Resilience of Tropical Maize

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Abstract: Changes in soil-plant-water interactions and rising drought frequency are major impacts of climate change, especially on maize, which is very sensitive to climate change in the tropics. The present research aims to explore the changes in functional traits, soil hydraulic properties and drought resilience under different intensities of drought. A randomized complete block design with five replications per treatment was used in the controlled field experiment, which was carried out in southern Nigeria for 112 days (16 weeks). Irrigation was varied for each treatment to cover rain regimes ranging from control to mild, moderate and severe drought. At weekly intervals and at harvest, the following climatic variables, soil moisture, traits of maize, soil hydraulic properties and crop performance were measured. Statistical analysis (ANOVA) was used to assess the effects of treatment. Result showed that the drought condition led to an increase in air and soil temperature, a decrease in soil moisture and soil humidity. Maize exhibited adaptive responses such as stomatal closure, root growth and thickening of the tissues, leading to better water use efficiency. The effect of drought on the soil hydraulic properties is clearly shown by a reduction in field capacity, an increase in wilting point and a reduction in hydraulic conductivity. The biomass reduction ranged up to 48%, and a significant reduction was observed in survival and drought resistance index in the worst cases. There was also an extreme reduction in grain yield to 2.2 ± 0.4 t/ha with a severe limitation in reproduction. Physiological adaptation to drought, as water use efficiency increased with drought. The results indicate that climatic, soil and plant variables interact in a complex way in drought resilience, and integrated management practices such as drought-tolerant crops and precision irrigation will be crucial to ensure maize production under climate variability.

Keywords: Climate Change, Drought Stress, Randomized Complete Block Design, Soil Moisture Dynamics, Water Use Efficiency, Tropical Agriculture.

1. INTRODUCTION

Climate change is one of the most formidable challenges of the 21st century for food systems globally and already has a significant impact in the tropics where production, including that of maize, is constrained by environmental variability. There are increasing disruptions in the finely tuned soil-plant-water interactions that regulate maize growth and survival due to increasing temperatures, unpredictable rains, and projected extended droughts [1-4]. Drought is one of the most disastrous climatic stressors that puts tropical agriculture at risk of severe losses in maize production and food security in sub-Saharan Africa and other arid tropical habitats [5-9]. Plant physiological response to drought stress is a dynamic relationship. Maize copes with water deficit by an orchestrated set of functional trait adaptations that transcend aboveground and belowground [10-12]. The adaptive strategy of the maize plant to maintain an optimum balance between water saving and carbon fixing has been known to change with varying soil moisture availability, such as stomatal conductance, leaf area and specific leaf area, chlorophyll content and root architecture [13-17]. Maize responses at the trait level are not independent but highly linked to soil hydraulic properties that govern water flow through the soil profile and the availability of water to the roots, including field capacity, permanent wilting point, available water content, and hydraulic conductivity [3, 18].

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These dynamics are interrelated, and their understanding is important in determining drought resilience in tropical maize cropping systems. Drought resilience not only includes the capacity of maize to survive water stress but also includes the capacity of the crop to survive and attain a desirable level of biomass, grain, and reproductive efficiency as compared to the well-watered condition [19-21]. In tropical agriculture, where smallholder farmers are especially susceptible to climate variability and have limited irrigation infrastructure, to construct drought-resilient maize systems, there is a need to know how climate-driven changes are converted into changes in maize functional properties and soil-water relationships [22]. As climate change has become a more pressing challenge to agricultural productivity, especially in drought-stricken conditions, increased attention has been paid to drought resilience in crop systems during the last few decades.

While significant research has been undertaken on the role of functional traits in mediating responses to drought in plants there are still some constraints that impede the formulation of comprehensive drought management strategies. Available literature on the subject is deficient in studies that simultaneously address the multi-dimensional effects of climatic variables, functional traits of maize, soil hydraulic properties, and crop performance in controlled but field-realistic tropical environments [23]. The available literature often concentrated on either plant physiology or soil physics alone, with knowledge gaps critical in understanding the co-response of these two systems to increasingly severe drought stresses [24-26]. Also, controlled gradient experiments that are also conducted through studies that enable systematic comparison at well-defined drought intensity levels are especially limited in tropical sub-Saharan settings [27].

The current studies generally focus on either physiological response to plants or physical properties of soils. For example, many studies have documented physiological responses of the plants under drought stress, such as stomatal conductance, Leaf Area Index (LAI), Chlorophyll content (SPAD) etc., [13-14]. On the other hand, some have concentrated on soil hydrologic characteristics alone, without considering plant reactions [18]. The silo approach narrows the vision for a holistic grasp of complex interactions between plant traits and soil-water dynamics, both of which play important roles in drought resilience.

Moreover, the majority of the research reported so far has been done under controlled laboratory or greenhouse conditions, and has been scarcely tested in a tropical smallholder production system. Field studies frequently do not include a systematic range of well-defined drought intensity gradients, which often contributes to a lack of understanding of threshold drought levels where crop or soil responses can no longer be reversed [27].

The above studies have reported conflicting results regarding the adaptation strategies of crops to drought. This indicates that the results of the studies discussed above on drought stress response of crops are inconsistent. Research to date can sometimes indicate the effectiveness of specific practices, e.g., drought-tolerant varieties or particular fertilization methods, to boost resilience; other research has led to other or even conflicting findings. The differences between the results highlight the complexity of plant responses to drought stress and the fact that there is no universal solution. Different forms of adaptation strategies may have mixed effects, depending on the crop type, environmental conditions, and management practices, so the scientific evidence is somewhat contradictory. For instance, some research indicates that greater root development facilitates water uptake and drought resistance [28], while others suggest that extensive root growth can reduce aboveground biomass and productivity, particularly during severe droughts [29]. Similarly, while early stomatal closure may significantly reduce carbon assimilation [30], some research suggests that stomatal closure can be used to effectively conserve water while having a minimal impact on photosynthesis [31]. The divergent results of these studies are illustrative of the context-dependent and complex nature of drought responses and the need for integrative multi-dimensional studies.

Consequently, there are existing knowledge gaps that still need to be addressed. First, there is limited understanding of the interaction between functional trait plasticity and soil hydraulic properties at varying intensities of drought in real world tropical farming systems. Most studies have considered plant physiology or soil physics, but neither the dynamic interactions between them. Second, thresholds for severity of drought that cause irreversible damage or changes in adaptive strategies are not well understood, particularly in smallholder tropical systems where management options are limited by resources. Third, the soil-water-plant feedback processes that influence drought resilience are under-researched and under-understood, especially the potential of integrated management practices to increase adaptive capacity.

This work fills these gaps by using a novel, field-based, gradient-drought experiment to concurrently explore the multi-dimensional response of maize in both functional traits, soil hydraulic parameters and crop performance in a tropical smallholder environment. Our multi-disciplinary approach not only integrates plant and soil responses, which is the focus of much previous research, but also accounts for the complex interaction that leads to drought resilience. In addition, this research introduces novel insights into thresholds for making systems more and more vulnerable to droughts, by establishing well-defined drought intensity levels that represent climate variability in southern Nigeria. This study, to our knowledge, is the first to quantify the combined effects of climate-induced drought on maize functional trait plasticity, soil-water relations and crop productivity in an on-farm tropical setting, thereby yielding important empirical data to guide sustainable drought management strategies.

Thus, the objectives of this work were to investigate the effect of drought on functional trait dynamics, and the relation between the same and hydraulic properties of soils, water use efficiency, and maize production under four drought conditions (randomized complete block design) representative of the southern region of Nigeria under an on-farm tropical field experiment. The aims were to (i) describe the temporal variations in important climatic variables and soil moisture dynamics under drought treatments, (ii) characterize the adaptive response of maize functional traits to increasing drought stress, (iii) characterize the changes in soil hydraulic properties and water use efficiency under drought conditions and (iv) quantify the overall effect of drought intensity on maize productivity and drought indicators of functional traits of maize as biomass yield, grain yield, harvest index, drought tolerance index and survival rate. The study was guided by the following hypotheses:

i. Soil hydraulic properties such as field capacity and hydraulic conductivity will be greatly reduced as drought intensifies.
ii. Higher Water Use Efficiency in drought conditions will be achieved by plants that have a higher functional trait plasticity.
iii. The grain yield of maize will be reduced as the intensity of the drought increases, and biomass will be reduced as grain yield is reduced, for a given intensity of the drought.

2. MATERIALS AND METHODS

2.1. The Study Site

This study was undertaken to examine the climate-induced changes in functional trait dynamics of soil-plant-water interfaces and drought resilience in tropical maize agriculture through a controlled field experiment. The experiment was conducted in Agbor under tropical environmental conditions, approximately at Latitude 6.25375° N and Longitude is 6.1942° E, on an elevation of about 70 metres above sea level. The region experiences on average about 1500–2000 mm of rainfall per annum. The annual mean temperature varies from 26 °C to 29 °C and in the study, average temperature during the experiment ranged from 28.5 °C to 34.1 °C according to the severity of the drought.

2.1.1. Soil characteristics

Agbor lies in the rain forest zone with high rainfall (> 2000 mm/year), long wet season and high humidity which influence the chemical profile of the soil. The soil of the experimental site at Agbor, Delta State, Nigeria was mostly sandy clay loam to loam in texture [32] and has moderate levels of organic matter typical of cultivated Ultisols in the humid forest-savannah transition zone. Specific properties of chemical properties are:

2.1.1.1. Organic matter content: The results of the physicochemical examination of soils in the various locations of Agbor and its adjoining communities indicated that the content of organic carbon, organic matter and Nitrogen in the eleven sample locations were not significantly different. The organic matter content in Agbor, Ika South LGA, falls into the category of medium with a mean content of approximately 2.54% for the area. The moderate level of organic matter is consistent with the rainforest favourable zone of Nigeria, which have higher levels of total nitrogen and organic carbon, contributing to fertility, along with higher organic matter.

2.1.1.2. pH: Soils in Agbor in Ika South LGA are slightly acidic having pH range of 6.61. The acidity is fairly moderate and it is typical of the humid tropical environment of the region and is fit for most crops. It is in contrast to the oil producing neighbouring LGAs where a high acidity was reported.

2.1.1.3. Nutrient levels: The nitrogen content is high in Ika South (0.27%) while the phosphorus content is medium (approx. 16.98 mg/kg), and the potassium, sodium, calcium and magnesium content is all high in Ika South area. In Agbor, however, the calcium content of the soils sampled were not the same but ranged from 0.08% to 0.14% with some spatial variations within the town.

2.2. Field Layout

Randomized complete block design (RCBD) was engaged with four treatments that are related to the intensity of drought, that is, control (ambient condition), mild drought, moderate drought, and severe drought. The experiment was replicated five times, making a total of twenty experiment units. The plots were 3 m by 3 m with a buffer zone in between to ensure that there was no movement of water between treatments. The drought conditions were implemented through a controlled irrigation regime whereby the amount of water to be applied was changed weekly in order to replicate the natural rainfall gradients: full irrigation on control plots and gradually decreasing the amount of water applied (around 60, 35, and 10 percent of field capacity) to mild, moderate, and severe drought conditions respectively.

2.2.1. Planting material

The study used a hybrid maize variety (ART/98/SW6-1-1 BB) from the Drought Tolerant Maize for Africa (DTMA) breeding program in Nigeria's drought trials obtained from the International Institute for Tropical Agriculture (IITA) Ibadan.

2.2.2. Experimental duration

The duration of the experiment was approximately 112 days (or 16 weeks) spanning over one cropping season, from February to May. This is the timeframe of the late dry to early wet season for better tropical maize varieties grown in southern Nigeria which have a maturity period of 90-120 days based on the extra-early and early maturing varieties [33-34].

2.2.3. Sampling procedure

Climatic data for the experiment were recorded by observing weekly air temperature and relative humidity with the help of Digital thermo-hygrometer kept at 1.5 m height above ground in each plot. Calibrated rain gauges (counting at least 500 ml) installed in unobstructed locations were used to measure rainfall, and weekly observations were made. There were 3 replications per plot to minimize spatial variability, and soil temperature measurements were taken weekly at 10 cm depth on each plot using soil thermometers and the average temperature was computed for each plot. A Time Domain Reflectometry (TDR) probe was used as demonstrated by Yan *et al*. [35] and Comegna *et al*. [36] to estimate the volumetric soil moisture at 10 cm depth every week, and three soil samples were taken on each plot to calculate a mean value.

Soil hydraulic properties were saved at the start and end of the experiment at the upper profile (0-20 cm). Three representative samples were obtained from each treatment by combining four random cores from each plot. Laboratory tests were performed for field capacity, permanent wilting point (PWP) with pressure plate and hydraulic conductivity with constant head permeameter as described in the methodology by Angelaki *et al*. [37]. The plant functional traits were evaluated by three sampling time points: the vegetative growth stage and two stages of the reproductive growth stage. Leaf area was determined with a leaf area meter and several leaves (5-10) were harvested from each plant and averaged. To reduce diurnal effects, stomatal conductance was measured using a steady state porometer on the abaxial surface of at least three plants per plot, with measurements taken around the same time.

Root length density (RLD) was determined by sampling three soil cores (5 cm diameter x 20 cm depth) at random positions, washing away the soil from the root and then using image processing software to analyse the root. The Specific Leaf Area (SLA) was determined by measuring the leaf area and after oven-drying the samples, calculating their dry mass. The SPAD meter was used for the assessment of the chlorophyll content, taking three readings per leaf on average.

Three plants were randomly harvested from each plot at harvest for dry biomass and grain yield. For biomass estimation plants were cut at the ground level, dried at 70 °C to a constant weight, and weighed. Grains were threshed, dried and weighed at a standard moisture content (~12%) to determine yield. Harvest index calculated as the ratio of grain yield to total biomass, and was expressed as a percentage. The drought tolerance index was determined from the ratio of yield under drought stress and yield under control environment and the survival rate, which was obtained from the number of plants that survived to harvest and the number of plants that were originally planted.

The apparatus used in the laboratory were: pressure plate apparatus for measuring soil water retention, constant head permeameter for measuring hydraulic conductivity, precision balances for weighing plant and soil samples, and 70 °C oven for drying soil samples. Additionally, root analysis was performed using sieves, washing trays and imaging technology for measuring the root length. A leaf area meter (LICOR LI-3000C) and a steady-state porometer (SC-1 Leaf Porometer) and a chlorophyll meter (Konica Minolta SPAD-502) were used for plant trait measurements, calibrated rain gauges, soil thermometers and TDR probes for environmental measurements, providing accurate and consistent data collection across all study.

2.2.4. Maintenance of field capacity

Field capacity was established through a controlled irrigation method aimed at simulating a natural rainfall gradient, ensuring uniform soil water content across different drought treatment plots. This initial field capacity was defined in a laboratory setting before the experiment began. Weekly irrigation was conducted to maintain target soil moisture levels, informed by real-time data from TDR probes. The plots received varying amounts of water to correspond with specific drought conditions: control plants at field capacity (36.5%); mild drought at 60%; moderate drought at 35%; and severe drought at 10% of field capacity.

2.2.5. Water monitoring

Soil water was monitored weekly using TDR probes positioned at various locations within each plot to account for spatial variability. These probes provided immediate volumetric soil moisture readings, which were compared against desired moisture levels. If moisture was insufficient, additional water was applied to meet the targets. The Irrigation method was calibrated watering cans, ensuring equal water distribution among plots. All water applied was meticulously recorded, along with weekly water usage per treatment level. In addition to soil moisture, soil temperature and environmental conditions, including evaporation, were continuously monitored to assess their impact on water retention in the soil, allowing for adjustments in watering rates required to uphold treatment conditions throughout the experiment.

2.3. Data Collection

Specific leaf area (cm^2/g) was calculated as the quotient of leaf area to dry leaf mass, and chlorophyll content was determined by a SPAD chlorophyll meter. Standard laboratory procedures were used to determine soil hydraulic properties. A pressure plate apparatus at 33 kPa and 1500 kPa was used to estimate the field capacity and permanent wilting point, respectively. Available water content = Field capacity - permanent wilting point. The constant head permeameter method according to Diminescu *et al.* [38] was used to measure hydraulic conductivity (cm/hr). The water use efficiency (g biomass/kg water) was determined as the proportion of total dry maize biomass to the total water used in the plot during the period of the experiment.

At harvest, crop performance indicators were measured. The above-ground biomass yield (t/ha) was calculated by drying samples of maize plants in the oven to a constant weight. The grain yield (t/ha) was obtained following the drying and threshing process to standard moisture content. The ratio between the maize grain yield and the total biomass yield multiplied by 100 was taken as the harvest index of maize. The drought tolerance index was calculated by dividing the maize yield in the stress environment by the yield in the controlled environment. The survival rate (percent) was calculated as the percentage of maize plants that survived to harvest.

A digital thermo-hygrometer was used to measure climatic parameters such as air temperature (°C) and relative humidity (percentage) and a set of calibrated rain gauges to simulate and measure rainfall (mm/week). The soil temperature was determined by inserting soil thermometers at the depth of 10 cm and the soil moisture content was weekly measured using soil moisture probe (Time Domain Reflectometry, TDR method) as demonstrated by Yan *et al*. [35] and Comegna *et al*. [36]. The maize functional traits were determined at appropriate vegetative growth. The measurement of leaf area (cm^2) was done on a leaf area meter. A steady-state porometer was used to measure stomatal conductance (mmol m^{-2} s^{-1}). Root length density (cm/cm^3) was determined by sampling the soil in core samples and washing roots and analysis of the images.

2.4. Data Analysis

A two-way Analysis of Variance (ANOVA) was used to test the differences among treatments and block effects, and a significance level of $P < 0.05$ was used. The statistical analysis was done with the help of the standard statistical software (SPSS), and the results were given in terms of mean and standard deviation. The statistical model used was:
$Y_{ij} = \mu + T_i + B_j + \varepsilon_{ij}$
where:

- T_i = drought treatment effect
- B_j = block effect
- ε_{ij} = residual error

3. RESULTS AND DISCUSSION

Climatic parameters and soil moisture variations which have been varying with the intensification of the drought conditions are presented in Table 1 and have been seen to be showing a gradational trend for the various parameters. Under the control (ambient) condition is an environment that is as close as possible to the ideal tropical growing conditions. Mean temperature was somewhat moderate at 28.5 +/- 0.6 °C with a high weekly rainfall of 45.2 +/- 3.1 mm and a high relative humidity of 78.4 +/- 2.5%. These conditions resulted in a good maintenance of the high soil moisture content (32.1 ± 1.8), with the soil temperature being kept slightly low at 27.3 ± 0.7 °C, which effectively reduced the soil temperature through evaporative cooling and provided adequate soil water supply in the profile.

Climatic change can be observed as conditions change to mild drought. The mean temperature rose to 30.2 ± 0.8 °C while the rainfall decreased significantly by around 43% to 25.6 ± 2.4 mm/week compared with the control. In addition, there was a decrease in relative humidity of 70.1 ± 2.9 which indicates the drier weather. This resulted in a reduction of the moisture content of the soil to 24.7 ± 1.5, or less water was available to the plants. The moisture content of the soil was also lower and, in turn, the temperature of the soil reached 29.0 ± 0.6 °C.

At moderate drought, the trends were further intensified. The mean temperature was 32.0 ± 0.9 °C and the rainfall (less than the control) was 12.8 ± 1.7 mm/week. This decreased the relative humidity to 62.5 ± 3.3. The soil moisture was reduced to 18.3 ± 1.2, which means that there was a significant loss of plant-available water. Meanwhile, the soil temperature has increased to 30.6 ± 0.8 °C, which

Table 1. Climatic variables and soil moisture dynamics across treatments.

Treatment	Mean Temp (°C)	Rainfall (mm/week)	Relative Humidity (%)	Soil Moisture (%)	Soil Temperature (°C)
Control (Ambient)	28.5 ± 0.6	45.2 ± 3.1	78.4 ± 2.5	32.1 ± 1.8	27.3 ± 0.7
Mild Drought	30.2 ± 0.8	25.6 ± 2.4	70.1 ± 2.9	24.7 ± 1.5	29.0 ± 0.6
Moderate Drought	32.0 ± 0.9	12.8 ± 1.7	62.5 ± 3.3	18.3 ± 1.2	30.6 ± 0.8
Severe Drought	34.1 ± 1.1	4.5 ± 0.9	55.2 ± 2.8	10.6 ± 0.9	32.4 ± 1.0

emphasized that the soils with less moisture content have a greater capacity to heat up. The system experienced extreme conditions of stress in the severe drought treatment. The relative humidity was also lowered to 55.2 ± 2.8 further reinforcing the dryness of the atmosphere. Soil water status was at a critical level of 10.6 ± 0.9% (about one-third of the control) water status, which was very limiting for plant water uptake. In this context the soil temperature increased to 32.4 ± 1.0 °C which was the maximum in all the soil treatments as there was less evaporative cooling and more absorption of the solar heat from the soil.

In general, the table shows a correlated trend: with the increase in the severity of drought, the temperature and soil temperature increased while rainfall, relative humidity, and soil moisture decreased drastically. These intertwined processes demonstrate that climate-induced drought can have a dual influence on the atmosphere and soil water levels and lead to more and more stressful environments that can influence the growth and survival of plants in tropical farming. This is in line with the reports of Matlaga *et al*. [39] who reported that increasing drought will favour species with more conservative traits, resulting in greater survival in low soil moisture conditions, Haghpanah *et al*. [40] who observed that plants exhibit various physiological and molecular responses to drought stress, enabling them to adapt and maintain crop resilience in limited water environments, and Sato *et al*. [41] who documented that drought stress reshapes atmospheric conditions, depletes soil water reserves, and reduces plant growth and survival in tropical and rain fed systems.

Table 2 shows that the growth in drought stress triggers the synchronous alterations in the functional traits of plants, which indicates adaptive responses as well as physiological constraints during water scarcity. Plants have optimum growth characteristics under the control condition. The maximum leaf area was 145.6 ± 5.2 cm^2 which shows that the photosynthetic areas are large. The stomatal conductance was also relatively high (320.4 ± 15.1 mmol m-2 s-1), allowing for an efficient gas exchange and carbon incorporation. The low value of root length density (1.85 +- 0.12 cm/cm^3) shows that the soil does not need to be explored too deep, since there was enough water available. Specific leaf area (SLA) was also found to be highest (210.5 ± 8.4 cm^2/g) indicating a low leaf thickness and resource-acquisitive leaves, and chlorophyll content (48.3 ± 2.1 SPAD) was the highest, which is an indicator of high photosynthetic rate.

The leaf area reduced to 130.2 + 4.8 cm^2, which means that the surface area was reduced to minimize water loss by transpiration. Stomatal conductance reduced to 275.3 ± 13.7 mmol m^{-2} s^{-1}, which indicates a partial stomatal closure in order to conserve water. However, in contrast, the growth of root length density increased to 2.10 ± 0.15 cm/cm^3, indicating higher proliferation of roots to search down to the deep or limited soil water. The leaves were thicker (SLA reduced to 195.7 ± 7.9 cm^2/g), as is typical in thicker leaves, which tend to be more resistant to drying. Chlorophyll level also decreased to 44.9 ± 2.4 SPAD, which presupposes a minor decrease in photosynthetic activity.

These trends were heightened under moderate drought. The leaf area decreased further to 110.5 ± 5.6 cm^2, and there was a further strategy of minimizing water loss. Stomatal conductance reduced to 275.3 ± 13.7 mmol m^{-2} s^{-1}, which indicates a partial stomatal closure in order to conserve water. However, in contrast, the growth of root length density increased to 2.10 ± 0.15 cm/cm^3, indicating higher proliferation of roots to search down to the deep or limited soil water. The leaves were thicker (SLA reduced to 195.7 ± 7.9 cm^2/g), as is typical in thicker leaves, which tend to

Table 2. Plant functional traits under climate stress conditions.

Treatment	Leaf Area (cm^2)	Stomatal Conductance (mmol m^{-2} s^{-1})	Root Length Density (cm/cm^3)	Specific Leaf Area (cm^2/g)	Chlorophyll Content (SPAD)
Control	145.6 ± 5.2	320.4 ± 15.1	1.85 ± 0.12	210.5 ± 8.4	48.3 ± 2.1
Mild Drought	130.2 ± 4.8	275.3 ± 13.7	2.10 ± 0.15	195.7 ± 7.9	44.9 ± 2.4
Moderate Drought	110.5 ± 5.6	210.6 ± 12.9	2.45 ± 0.18	180.2 ± 6.5	40.7 ± 2.7
Severe Drought	85.3 ± 6.1	145.8 ± 10.3	2.90 ± 0.21	160.8 ± 5.9	35.2 ± 3.0

be more resistant to drying. Chlorophyll level also decreased to 44.9 ± 2.4 SPAD, which presupposes a minor decrease in photosynthetic activity.

Plants under extreme stress conditions are those in severe drought conditions. The leaf area decreased drastically to 85.3 ± 6.1 cm^2, almost 40 percent that of the control with a severe limiting effect on photosynthetic surface. Stomatal conductance also reduced to 145.8 ± 10.3 mmol m^{-2} s^{-1}, which shows that stomata were strongly closed and the carbon uptake was limited. On the other hand, root length density was highest at 2.90 ± 0.21 cm/cm^3, indicating a strong movement towards water foraging of the soil. The reduction in specific leaf area further to 160.8 ± 5.9 cm^2/g proves that thicker leaves were developed and more resistant to the drought. The lowest value of chlorophyll content (35.2 ± 3.0 SPAD) could be as a result of significant damage to the photosynthetic machinery.

On the whole, these results show a well-defined trade-off in the conditions of drought stress. The aboveground traits (leaf area, stomatal conductance, chlorophyll content, and SLA) decreased in a certain order, which entails the decrease in photosynthetic capacity and growth and the increase in belowground investment (root length density), which indicates an adaptive strategy to improve water uptake. Zahedi *et al*. [42] noted that these organized changes in traits show how plants trade-off between conserving water and getting resources to enhance their survival under the increasingly harsh conditions of drought.

Figure1 shows the reactions of some important physiological, soil and productivity parameters of maize to the four drought treatments (Control, Mild, Moderate and Severe) applied, represented by 100% Field Capacity, 75% FC, 50% FC and 25% FC respectively. As seen in the trends, the higher the drought stress, the more impact it has on crop performance.

The soil water content was reduced gradually with the control treatment having 32.1% while the severe drought treatment had 10.6%, indicating the establishment of a drought gradient. Similarly, there was a decrease in relative leaf water content from 89.2% to 45.8%, which corresponds to the increasing water deficit of plants during the drought.

The soil temperature, however, rose gradually from 26.5 °C to 34.8 °C; this was a result of less cooling effect when the soil was dry. Likewise, the growth of maize root length density was higher, from 0.85 cm/ cm^3 under control to 2.90 cm/ cm^3 under severe drought, thus indicating that maize invested more in their roots to enhance the use of water under drought conditions.

Water use efficiency (WUE) is also increased with increasing stress gradually from 3.25 to 4.20 g biomass kg water, suggesting that the plants were

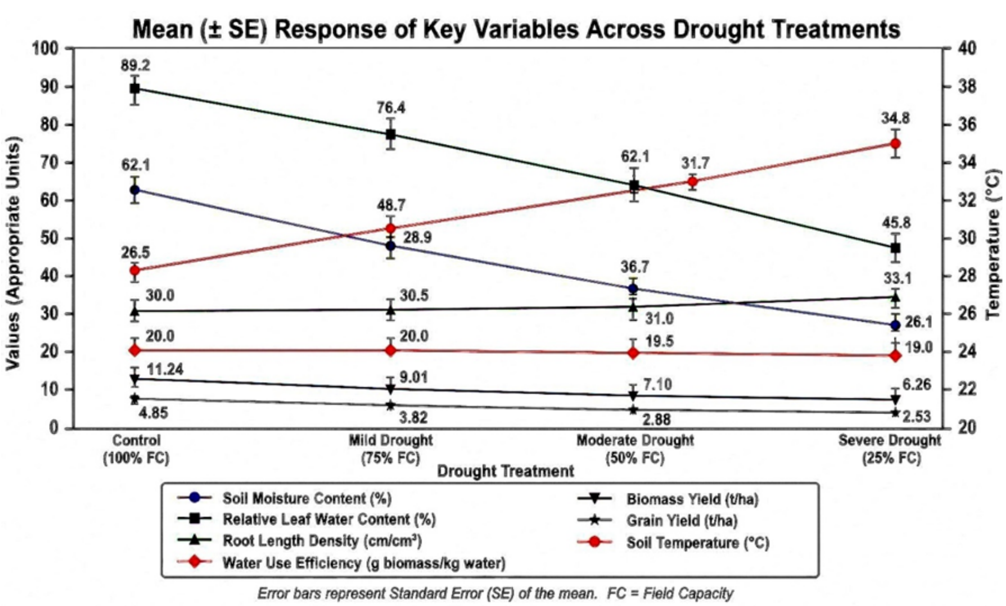

Fig.1. Mean ± SE Response of key variables across drought treatments.

utilizing available water with increasing efficiency. But this physiological change did not keep productivity losses low. As the drought severity increased, the biomass yield reduced from 11.24 to 6.26 t ha^{-1} and the yield of grain reduced from 4.85 to 2.53 t ha^{-1}.

As a whole, the graph indicates a substantial decrease of soil moisture, plant water status, biomass and grain yield with increasing drought stress, as well as a greater rooting and water use efficiency, and rising soil temperature. The trends show that while maize can cope physiologically due to drought, this ability is not enough to compensate for the potential negative impacts of drought with a severe water deficit on crop productivity.

As a general rule, Figure 1 indicates that drought reduced water holding capacity of the soil (field capacity), increased water holding capacity at inaccessible depths (PWP), and decreased water movement (hydraulic conductivity), thus significantly reducing the water supply. Water use efficiency, on the other hand, rose steadily as a measure of an adaptive response of the plant to make the most of scarce water resources as observed by Li *et al*. [43]. This brings out a major mechanism of drought resilience in tropical agriculture, which includes a change of resource abundance strategies of plants to water conservation and efficiency strategies when the environment is under stress.

The impact of augmented drought stress on crop productivity and resilience is depicted in Table 3, where there were evident decreases in yield and existence as well as adjustments in allocation efficiency. With the condition of control, crop performance was ideal. The biomass yield was 8.5 ± 0.4 t/ha with a grain yield of 4.2 ± 0.3 t/ha, which indicates high productivity. The harvest index (HI) was 49.4 ± 2.1, which implies that almost half of the total biomass was efficiently utilized to produce the economic yield (grain). The survival rate of 98.5 ± 1.2 is a low stress level, and the drought tolerance index (DTI) standardized was 1.00 (the point of reference). In case of mild drought, productivity was reduced moderately. The biomass yield reduced to 7.6 ± 0.5 t/ha, and grain yield reduced slightly to 3.8 ± 0.2 t/ha, which suggests approximately a 10% reduction compared to the control. Interestingly, there is a slight increase in harvest index to 50.0 ± 1.8%, which implies that the proportion of biomass to grain remains or is slightly improved, although the total growth was minimal. The biomass yield was decreased to 6.2 ± 0.6 t/ha, a significant decrease of around 27%, when compared to the control. The grain yields also went down to 3.1 ± 0.3 t/ha. However, the harvest index (50.3 ± 2.0%) was not significantly influenced, indicating that plants still place importance on reproductive productivity even under stressful conditions. DTI was reduced to 0.74, indicating a lesser tolerance to drought. The survival percentage was reduced to 88.7 ± 2.3, which means that more plants might have died. Crop performance was badly affected by the extreme drought condition.

The biomass yield was reduced dramatically to 4.8 ± 0.7 t/ha or almost 44% lower than the control. There was also an extreme reduction in grain yield to 2.2 ± 0.4 t/ha with a severe limitation in reproduction. In contrast to the previous stages, the harvest index was reduced to 45.8 ± 2.5%, indicating that plants cannot allocate biomass efficiently to grain production in the case of extreme stress. The DTI was reduced to 0.52, exhibiting low drought tolerance, and the survival rate also decreased significantly to 76.3 ± 3.1, showing that a lot of plants were lost.

Table 3 indicates that with the escalation in the severity of drought, biomass yield, grain yield, drought tolerance, and survival rate change progressively. Although the harvest index was maintained or slightly improved with mild to moderate drought conditions, which are signs of

Table 3. Crop performance and drought resilience indicators.

Treatment	Biomass Yield (t/ha)	Grain Yield (t/ha)	Harvest Index (%)	Drought Tolerance Index	Survival Rate (%)
Control	8.5 ± 0.4	4.2 ± 0.3	49.4 ± 2.1	1.00	98.5 ± 1.2
Mild Drought	7.6 ± 0.5	3.8 ± 0.2	50.0 ± 1.8	0.91	94.2 ± 1.6
Moderate Drought	6.2 ± 0.6	3.1 ± 0.3	50.3 ± 2.0	0.74	88.7 ± 2.3
Severe Drought	4.8 ± 0.7	2.2 ± 0.4	45.8 ± 2.5	0.52	76.3 ± 3.1

adaptive use of allocation strategy, it was reduced in the case of severe drought, which is an indication of physiological breakdown, as buttressed by Jarin *et al*. [44]. These findings demonstrate that, as well as growth, drought also impedes and impairs plant survival and reproductive output in tropical agricultural systems.

Treatment Effects (Drought Level): The combined ANOVA results for crop performance and drought resilience indicators are given in Table 4. The F-tests for drought treatment were all highly significant for Biomass Yield ($F = 27.62$, $p < 0.0001$), Grain Yield ($F = 23.70$, $p < 0.0001$), Drought Tolerance Index ($F = 49.61$, $p < 0.0001$) and Survival Rate ($F = 35.31$, $p < 0.0001$), indicating that progressive drought stress caused significant and substantial reductions in crop performance. The treatment also had a significant effect on Harvest Index ($F = 4.66$, $p = 0.022$) although it was less strong, indicating partial maintenance of biomass partitioning to grain under mild to moderate stress.

Block Effects (Replication): No significant block effect was observed with all the response variables (for all variables, $F = 0.85$ and $p = 0.522$) and thus the spatial variations in the five replication blocks were negligible and did not affect the treatment comparisons. This confirms that there were no other sources of field variability besides the treatments such that the experimental layout is valid, and that the RCBD design was successful in controlling any

Table 4. Combined ANOVA results for crop performance and drought resilience indicators.

Response Variable	Source of Variation	Df	SS	MS	F	p-value	Sig.
Biomass Yield (t/ha)	Treatment (Drought Level)	3	32.4800	10.8267	27.62	< 0.0001	***
	Block (Replication)	4	1.3266	0.3317	0.85	0.522	Ns
	Error	12	4.7034	0.3920	—	—	—
	Total	19	38.5100	—	—	—	—
Grain Yield (t/ha)	Treatment (Drought Level)	3	8.9200	2.9733	23.70	< 0.0001	***
	Block (Replication)	4	0.4246	0.1061	0.85	0.522	Ns
	Error	12	1.5054	0.1254	—	—	—
	Total	19	10.8500	—	—	—	—
Harvest Index (%)	Treatment (Drought Level)	3	58.7700	19.5900	4.66	0.022	*
	Block (Replication)	4	14.2230	3.5558	0.85	0.522	Ns
	Error	12	50.4270	4.2023	—	—	—
	Total	19	123.4200	—	—	—	—
Drought Tolerance Index	Treatment (Drought Level)	3	0.4160	0.1387	49.61	< 0.0001	***
	Block (Replication)	4	0.0095	0.0024	0.85	0.522	Ns
	Error	12	0.0335	0.0028	—	—	—
	Total	19	0.4590	—	—	—	—
Survival Rate (%)	Treatment (Drought Level)	3	1210.6000	403.5333	35.31	< 0.0001	***
	Block (Replication)	4	38.6760	9.6690	0.85	0.522	Ns
	Error	12	137.1240	11.4270	—	—	—
	Total	19	1386.4000	—	—	—	—

Significance codes: *** $p < 0.001$; * $p < 0.05$; ns = not significant; df = degrees of freedom; SS = sum of squares; MS = mean square.
Error degrees of freedom: $df_{error} = (t - 1)(b - 1) = 3 \times 4 = 12$.

other source of field variability, which added to confidence of the treatment F-tests.

Correlation and Regression Analysis: Soil moisture and root density are inversely correlated and consistent with adaptive root proliferation during drought (Table 5). The results of the correlations analysis show that soil moisture decreases with increasing drought severity, whereas root density and WUE increase. In contrast, grain yield declined under severe drought conditions.

Regression Analysis: The regression analysis (Table 6) showed that soil moisture, root density, and water use efficiency (WUE) positively influenced the maize biomass yield. The biomass yield increased by about 0.22 t/ha for every 1% increase in soil moisture, while a one-unit increase in root density and WUE increased biomass yield by about 2.5 and 1.8 t/ha, respectively. Model fit, R^2, is close to 1, meaning that these variables account for almost all the variation in biomass yield between the different treatments. Water use efficiency was positively related to soil moisture, which is consistent with the hypothesis that plant water use efficiency will increase under water scarcity.

$$\text{Biomass Yield} = \beta 0 + \beta 1(\text{Soil Moisture}) + \beta 2(\text{Root Density}) + \beta 3(\text{WUE}) + \varepsilon$$

The findings of this study are strong indications that gradually increasing levels of drought stress lead to coordinated and quantifiable changes in climatic variables, maize functional attributes, soil hydraulic characteristics, and crop performance of a tropical maize agricultural system. The trends within the whole four experimental treatments were all indicators of the multidimensionality of the effects of drought and the adaptability of maize plants that work in water-restricted settings in the tropical setting of southern Nigeria. Similar results were recorded by Yawale *et al*. [45] who reported that cropping P4 x P9 and P3 x P4 genotypes significantly improved growth attributes under drought and heat stress conditions, potentially benefitting maize breeding programs in Nigeria. Fayose and Fakorede [33] further documented that 3 drought-tolerant maize varieties showed superior grain yield and kernel number, making them recommended for adapting to climate variability and change in Nigeria and Aboderin *et al*. [46] whose multi-environment evaluation results showed that drought and low nitrogen strongly depressed maize

Table 5. Results of correlation analysis.

Variable Pair	Approximate r*	Interpretation
Soil Moisture & Root Density	-0.99	Very strong negative correlation: as soil moisture decreases, root density increases markedly, indicating adaptive root proliferation under drought.
Soil Moisture & WUE	0.99	Very strong positive correlation: lower soil moisture stimulates higher WUE, supporting physiological adaptation hypotheses.
Soil Moisture & Yield	0.99	Very strong positive correlation: higher soil moisture correlates with higher biomass and grain yields.
Root Density & Yield	0.98	Very strong positive correlation: increased root density associates with higher yields, indicating effective water foraging.
WUE & Yield	0.97	Very strong positive correlation: better water use efficiency aligns with increased yield.

* Pearson's r between key variables across treatment means.

Table 6. Results of regression analysis.

Variable	Coefficient Estimate (approximate)
Intercept (β0)	12.0 (baseline yield at maximal moisture)
Soil Moisture (β1)	+0.22 (per % soil moisture)
Root Density (β2)	+2.5 (per cm/cm^3 root density)
WUE (β3)	+1.8 (per g biomass/kg water)

performance, while a subset of hybrids combined stress tolerance with useful yield across Nigerian environments.

The climatic and soil moisture results provided in Table 1 substantiate the success of the applied drought gradient and show a steady negative correlation between the severity of drought and the availability of the soil moisture in the fields of maize. The severe loss of soil moisture (reduced to 10.6% in severe drought against 32.1 percent in control conditions) and the increase in air and soil temperature are indicative of the type of compounding stress dynamics that are increasingly projected in a future climate context in sub-Saharan Africa. The simultaneous increase in temperature of soils when moisture decreased is in line with the long-established fact that wet soils cool more effectively by evaporation, whereas drier soils heat up and capture solar radiation better. These results support the perception that drought in tropical maize systems is not a phenomenon of only precipitation deficit but a complex climatic phenomenon that at the same time changes atmospheric, edaphic, and thermal conditions and creates an unfavourable environment for maize growth and survival.

The coherent responses to water stress are observed in the functional trait responses reported in Table 2, which represents a strategy of maize-level adaptation. The fact that the plant was experiencing a steady loss in leaf area, stomatal conductance, specific leaf area, and chlorophyll content and at the same time was experiencing a steady rise in root length density indicates the archetypal above-below-ground resource allocation trade-off that maize plants were engaging in during drought. One of the earliest and best-documented plant responses to water deficit was stomatal closure, which decreased conductance in the control conditions (320.4 mmol m^{-2} s^{-1}) to a level of 145.8 mmol m^{-2} s^{-1} under severe drought-more than 54% lower. Although this reaction saves water, it will necessarily limit CO_2 uptake and thus limit photosynthetic carbon gain, which is consistent with reports of Flexas *et al*. [24]. The corresponding decrease in specific leaf area indicates a structural compensation in favor of more water-storing leaves of maize, which are also known to be more resistant to dehydration in the cell. In the meantime, the significant growth of root length density, which peaks at 2.90 cm/cm^3 in the conditions of severe drought, is an indicator of compensatory investment in belowground water foraging a reaction in the larger context of functional trait plasticity as explained by Poorter *et al.* [16] and Reich [17]. These synchronized changes in traits together show how maize systems in the tropics change their priorities towards survival and water uptake at the expense of growth and photosynthetic efficiency in the face of increasing drought conditions.

The soil hydraulic data (Figure 1) gave valuable edaphic background information as to why maize responses were as strong as drought stress. The reduction in the field capacity of 36.5 to 30.6% and the corresponding increase in permanent wilting point of 14.2 to 18.8 percent along the drought gradient led to an approach of 50% in the available water content, to 22.3 to 11.8 percent. This reduction of the water window of maize plant-accessible water directly limits root water uptake whether or not roots grow, emphasizing that the adaptive traits of roots act within constraints placed by the physical characteristics of the soil. The gradual decline in hydraulic conductivity is also a sign that water flow within the soil matrix was becoming more and more limited in the later stages of drought, which could lead to spatial heterogeneity in water availability that must be overcome by the maize roots via architectural changes [41-43]. It is on this ground that the paradoxical rise in the efficiency of water use, which in turn is the rise of 3.25 g biomass/kg water under control conditions and 4.20 g biomass/kg water under severe drought, is an indication of a significant physiological maize adaptation. Instead of being a direct indicator of productivity, this increasing stress-induced efficiency indicates that the plant is partially decoupled in its biomass production and water usage via stomatal control and metabolic savings, which is in line with the drought resilience processes outlined by Blum [21] and Tardieu *et al*. [25].

Table 3 summarized the data of crop performance into agronomically significant results of maize, which are a result of these physiological and edaphic dynamics. The 44 % decrease in biomass production and the 48 % decrease in grain production during severe drought in comparison to the control are significant losses in productivity that have direct food security consequences to tropical smallholder maize agricultural frameworks [47-48]. A drought tolerance index of 0.52 in severe stress conditions reflects that not more than half of maize yield potential is achieved when water is severely limited, which explains the agronomic sense of urgency around the creation of drought-adapted maize varieties and water management systems [49-50]. Of special concern is the trend of the harvest index, which was fairly constant or slightly enhanced during mild and moderate drought and only dropped significantly in the case of severe stress. This trend indicates that initially maize plants maintain reproductive investment at the cost of vegetative growth, an adaptive trade-off that fails at extreme stresses when physiological capacity is exceeded in general as observed by Sheoran *et al*. [51], Yasin *et al*. [13] and Keya *et al*. [52]. The subsequent reduction of the survival rate to 76.3% during extreme drought also indicates the threshold nature of maize stress tolerance, whereby after it reaches a critical level, irreversible damage and mortality become the ultimate consequences.

Combined, the findings of this paper indicate that drought resilience among tropical maize is a consequence of the combined effects of atmospheric, physiological, and edaphic systems and not a specific adaptive process. According to the findings, it is necessary to have management interventions to deal with the retention and optimization of maize traits simultaneously, such as planting drought-tolerant maize varieties, improving soil organic matter to increase water-holding capacity, and having strategies of supplementing irrigation that are set at maize-specific water requirement levels. Nehe *et al.* [53] demonstrated that root architectural traits, including root depth and root number, contribute to drought adaptation by influencing the plant's capacity to access soil water under water-limited conditions. The study focuses on essential climate adaptation strategies to address climate change, highlighting the necessity for drought-resistant crop varieties, improved irrigation management, and effective soil moisture management techniques [54]. These strategies aim to enhance the resilience of drought-prone areas by fostering drought-tolerant ecosystems and ensuring more predictable crop yields amid shifting precipitation patterns. Additionally, crop models can assist in predicting plant responses under various climate scenarios, enriching the adaptation knowledge base.

On breeding, findings suggest significant potential in breeding programs to cultivate traits such as deeper root systems, water-use efficiency, and stress-responsive gene expression. This can be achieved through marker-assisted selection or genomic selection, underscoring the physiological and molecular aspects of drought resilience as critical factors in stress-specific breeding efforts [55].

Lastly, the study underscores the role of precision agriculture technologies like soil moisture sensors, remote sensing, and variable rate irrigation in optimizing water use and crop production during droughts [56]. These technologies help mitigate negative environmental impacts while enhancing resource management, yield stability, and sustainable exploitation in light of climate variability.

4. CONCLUSIONS

The results from this study showed that drought significantly affects soil-plant-water relations and maize productivity in tropical systems. A progressive increase in drought severity caused a coordinated response of climatic variables, maize functional traits and soil hydraulic properties, which resulted in a decrease in biomass and grain yields of up to 48%. Maize showed physiological resilience by closing stomata, increasing root surface area and thickening of tissues. Yet when the drought was severe, significant reductions in survival and yield traits were observed demonstrating the limit of drought resistance. The results highlighted the need for an integrated approach to drought coping (e.g. drought resistant maize varieties, better soil moisture use efficiency, and more accurate irrigation) to enhance drought resilience. Maize showed signs of physiological adaptability, but the losses in yield under extreme stress underscores the need for proactive measures. The overall results confirm that a multi-dimensional strategy including plant and soil systems is needed to maintain maize productivity in tropical areas in the face of climatic variability.

In light of the results of the present study, the following are some of the recommendations that are aimed at increasing the resilience of droughts in tropical maize systems, especially in moisture-stressed environments, like southern Nigeria. Implementation of maize varieties that are drought-tolerant: The breeding effort must focus on developing and implementing varieties of maize that have functional characteristics that have been shown to provide the crop with drought tolerance, such as high root length density, small specific leaf area during drought, efficient stomatal control, and the ability to retain acceptable harvest indices under moderate levels of water stress. Public extension systems should be given priority to provide farmers with easy access to such kinds of maize.

6. CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

7. ETHICAL STATEMENT

This work does not include any studies involving human or animal subjects. Only plant materials were involved; therefore, ethical approval was not required.

8. FUNDING

No funding was received for this work.

9. AUTHORSHIP CONTRIBUTION

All authors contributed equally to this study and the development of the manuscript.

10. DECLARATION

All authors declare the originality of results and copyright are assigned to the Pakistan Academy of Sciences.

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